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THE CALCIFEROUS GLANDS OF LUMBRICIDAE AND DIPLOCARDIA

WITH TWELVE PLATES

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INTRODUCTION

Certain organs related to the posterior part of the esophagus in earthworms belonging to the family Lumbricidae, and also in those of certain other systematic groups, have been studied and described at various times since the early part of the nineteenth century. These organs have received various names, of which calciferous glands, esophageal glands, and glands of Morren are among those more commonly used in the recent literature on the subject. The purpose in the preparation of this paper has been to bring together the more important results of the work of previous investigators who have studied the anatomy of such organs in the Lumbricidae; to add some facts gained from my own study of worms of this group; and to describe similar organs found in two new species of the genus Diplocardia which belongs to another family of earthworms. This involves the description of these two new species, but it is hoped that a better basis for an outline of the probable history of the development of the complicated structures in the Lumbricidae will result from the discussion of the interesting series of such organs found in the different species of Diplocardia. Among these species we find organs of a degree of complexity similar to that in Lumbricidae; others of a very simple type in which we have merely a few longitudinal folds instead of a complicated set of longitudinal tunnellike chambers; and several intermediate stages between these two extremes.

Preliminary to a discussion of the literature on the subject and to an attempt to trace the principal steps in the attainment of the present state of our knowledge of the anatomy of the calciferous glands, it is necessary to briefly summarize the principal facts of their structure, and explain the terminology used. In the Lumbricidae more commonly studied, the part of the esophagus which is included in somites 10-14, and is just anterior to the crop, is characterized by an extensive glandular development of the wall. This includes a pair of evaginated pouches in somite 10 which communicate through large apertures with the lumen of the esophagus. In the wall of the somites next following is a series of longitudinal tunnellike chambers which have their cavities continued into the posterior part of 10 where they are in communication with the large cavities of the paired pouches in that somite. Figure 17 illustrates the appearance of a transverse section, and figure 50 of a sagittal section through the wall of one side in this region. Longitudinal blood vessels extend along the margins of the lamellae which separate the longitudinal chambers, both along the inner

margins in close relation to the lining epithelium of the esophagus and also along the outer margins in close relation to the muscle layers of the esophagus. These vessels provide an extensive blood supply and account for frequent references to the reddish color. The chambers are much reduced in size in somite 14 and the diameter of the esophagus is correspondingly reduced. In a very few species including the much described *Lumbricus terrestris*, the lateral walls of the esophagus are considerably expanded in each of the somites 11 and 12 and this has led to the common practice of referring to three pairs of glands in somites 10, 11 and 12, when in reality we are dealing with what would more reasonably be considered as a single organ. The pouches in somite 10 are the first or anterior pair of glands and the lateral expansions in somites 11 and 12 are the second and third pairs mentioned in much of the literature, including most zoology text-books.

HISTORICAL

The following discussion of the literature, as well as of the worms themselves, is limited to facts of the general anatomy or structure and deals not at all with the details of histology or of physiology. These latter topics are of great interest and importance, but have received little attention from the writer who therefore has no contribution to make in these fields. The literature examined includes most of the papers commonly mentioned by writers dealing with the subject and probably all, or nearly all, of those making important contributions, but no claim is made for a complete study, nor that some really important contribution may not have been overlooked.

Any who are interested in the histology and physiology of the glands are referred to a paper by Stephenson and Prashad (1919) for a discussion of the literature on those subjects.

As a matter of convenience in the following discussion, the usual practice of treating the gland region as made up of several pairs of glands, instead of a single one, will be followed.

The first paper to receive attention is that by Julius Leo (1820), entitled De structura lumbrici terrestris. Dissertatio inauguralis.

Approximately 30 pages of text and two plates are given to a general description of *Lumbricus terrestris* and of another lumbricid of smaller size. The writer was much surprised at the amount of accurate information contained in Leo's paper and still more surprised, in reading the papers of later writers, to discover how little was known by most of them about the contents of Leo's paper. Since the original article may not be easily accessible to some who might be interested in its contents, that part of it which deals especially with the calciferous glands, and the two figures of especial interest are here reproduced.

"Superficiem externam oesophagi, corpuscula oblonga et subrufa occupant, utrinque tria (vid. Fig. VII. ff. gg.).[1] Descriptionem eorum addam.

"In medio oesophago sita sunt et tanta vasorum multitudine abundant ut in verme dum vivit secto pulsantia videantur, unde etiam a Willisio cor animalis dicebantur. Bina anteriora e duobus sacculis membranaceis constructa sunt, et orificia eorum oblonga in oesophago discernere licet: (vid. Fig. VII. ff.) et (Fig. VIII. c.)[2] concrementi albi terreo-salini granula continent. Quae supersunt corpuscula quatuor formam cylindraceam habent, et e striis albis longitudinalibus transversim plicatis, constructa sunt. Orificia horum corpusculorum in oesophago nunquam vidi, cum sacculis autem antecedentibus coniuncta mihi videbantur.

"Qui sit corpusculorum usus me fugit, cum in omnibus animalibus analogiam invenire non successerit. Analysis chemica materiae terreo-salinae, qua corpuscula anteriora repleta sunt, naturam harum partium forsitan docebit. Huius substantiae excretionem magni momenti esse, eamque forsitan digestionem promovere ex eo verisimillimum est, quod corpuscula sanguinis copia alia organa superant."

It will be noticed that Leo recognized the first pair of bodies as being saccular and provided with definite openings into the esophagus which he represented in his figure VIII and which is reproduced as figure 2 in this paper. He also recognized that the second and third pairs were different from the first pair in structure, and had a better idea of what that structure was than have some others who have written long since his time. He also expressed a correct opinion concerning the communication between the last two pairs and the first pair, and of the absence of openings from the last two pairs directly into the esophagus. Although his figures are very simple, they are more accurate than many that have been contributed by later writers. He made no statement that exactly located the organs in definite somites.

An extended review of this paper together with a plate, on which were reproduced seven of the ten figures of the original paper, appeared with the same title in Isis (1822, pp. 492-496, pl. IV.). This review contained merely a brief reference to the calciferous glands, and reproduced the two figures illustrating them. "Weiter hinten liegen auf der Speiseröhre 3 Paar braune Körper (Fig. 7, ff. gg.) in denen sich kalkige Körnchen finden, welche auch in der Zeichnung nicht gehörig abgesondert sind und deren Nutzen nicht errathen ist. Die 2 vorderen sind haütige Säckchen and öffnen sich in die Speiseröhre. Willis hielt diese Körper, weil sie ganz mit Blutgefässen durchzogen sind, für das Herz."

Later writers who have seen only this abstract have necessarily incomplete information of Leo's contribution to our knowledge of the subject.

[1] A drawing from this figure is reproduced as figure 3.

[2] A drawing from this figure is reproduced as figure 2.

A brief paper by Leo entitled "Ueber die Fortpflanzung der Regenwürmer" appeared in Isis, 1820, p. 386; and a brief review of it in London Magazine, 1823, p. 556. Nothing pertaining to the calciferous glands is contained in this paper, or in the review article. They are mentioned here since references to them have appeared in literature lists included in papers dealing with the glands together with other topics.

C. F. A. Morren (1826) contributed an extensive paper which described the results of his observations on various phases of anatomy, physiology, and natural history of *Lumbricus terrestris* and allied forms. With certain additions and emendations this appeared later as a paper of XV+280 pages and 32 plates (1829) under a different title. A copy of the paper in this latter form is the one consulted by the writer. On page 129 of this paper under the caption De glandulis oesophageis, we have the following brief and imperfect description:

"Praeter glandulas quas exhibet membrana de quâ modo egimus, adhuc existunt quatuor corpora glandulosa, maxime distincta, quae circumdant oesophagum versus tertiam ejus partem posteriorem, ubi ovaria inseruntur. Illa corpora quae naturae glandulosae arbitror, per paria sunt disposita: unum in utroque latere, ita ut omnia uno puncto conjungantur in canale ipso oesophagi, quod speciem crucis efformat, (vide *i et k, fig.* 1 *et* 2. *tab.* X. *bis*). Sunt plus minusve eminentes; color earum variat ab albo ad subflavum rubescentem; tunica est dura, aequalis, laevigata, humectata, etc.

"De usu harum glandularum non constat; praesertim quum consideramus hyeme durante et in multis juniorihus Lumbricis, nulla fere reperiri earum vestigia et saepe eas omnino desiderari. An pertinent ad organa generationis; an evolvuntur cum his tantummodo? Hunc nodum hìc solvere non valeo."

Figures 4 and 5 are copied from the portions of Morren's figures which represen,t the glands. He seems not to have seen the paper of Leo. On page 28c in a list of authors who had written on the Lumbricidae, there is a referene: Leo, (Lond. mag. Nov. 1823, p. 536 [should be 556]). On page 189, Leo's name is mentioned with an appended footnote giving the title of his paper with date 1822 and the following comment "Quod opus consulere mihi non datum fuit." In view of Leo's contribution to our knowledge of the calciferous glands, that of Morren seems practically valueless. The number and form of glands is given incorrectly; nothing is given of the details of their structure, nor of the relations which their cavities have with each other or with the lumen of the esophagus.

F. G. J. Henle (1835) in a paper devoted principally to other objects gave attention (p. 581) to the earthworm calciferous glands and referred to Leo with whom he agreed in his general account of the number of the glands and their relations to each other and to the esophagus. He made

no statement concerning the internal structure of the posterior two pairs, but commented on variations in their size due to variations in the amount of calcium salts contained.

E. Ray Lankester (1864 and 1865) published an article which appeared in three parts and dealt with the general anatomy of worms designated as *Lumbricus terrestris* and *L. agricola*. Part I on pages 263-268 contained the matter dealing with the alimentary tract and calciferous glands. It was accompanied by plate VII of which four figures were concerned with the glands. Lankester described three pairs of "oesophageal glands" of which the first pair were placed in the 11th somite (12 as enumerated by Lankester) and the other two pairs were placed in the next following somite. Of the first pair he says "They are firmly attached to the walls of the oesophagus, but do not appear to have any communication with its interior." He termed them pouches and stated that the wall is thin, and that they frequently contain crystalline bodies which are probably carbonate of lime. He stated that the second and third pairs differ from the first in form and appearance and that they are smaller, and their walls much thicker. They all have an "immensely vascular surface" due to numerous parallel longitudinal vessels and are often of "a bright red color." He described a very peculiar internal structure of all three pairs which is seen when a thin vertical section is made through them. His description and a figure indicate an interior "vascular region in which the blood vessels are arranged in loops."[3] No statement is made indicating that any communication exists between the cavities of any of the glands with each other or with the lumen of the esophagus. Lankester listed the review article of Leo's paper which appeared in Isis, 1822, but not the original article. Since he began his account by speaking of "three pairs of remarkable glands, which have never yet been described"; and mentioned Morren first in his account of the work that others had done on them, it seems reasonable to suppose that Leo's description had not been seen by him. The paper of Henle (1835) was not included in his bibliographic list nor mentioned in the discussion. Lankester's chief contribution was in his better figure of the superficial appearance of the glands and his description of the peripheral blood supply. His ideas of the relations of the gland cavities to each other and to the aesophageal lumen, and also of the structure of the second and third pairs of glands were less in conformity with facts than were those of Leo.

D'Udekem (1865) had a brief comment on the "glandes oesophagiennes." Both his brief description and a figure (7) show that he had an erroneous conception of their structure. His figure 2 shows more accurately the relative position of the glands and the associated lateral "hearts" than

[3] A drawing from this figure is reproduced as figure 7 and one from another one which has been copied in some modern text-books is reproduced as figure 6.

did a similar one of Lankester. He made no statements concerning their exact situation; nor concerning the relations of the cavities of the different glands to each other or to the esophageal lumen.

Claparède (1869) in a paper of about 60 pages and several plates published some important results of extensive histological studies of *Lumbricus terrestris*, and discussed in a thorough-going manner the published results of previous writers on the anatomy of Lumbricidae. By the use of more modern methods of technique and the study of transverse and longitudinal sections, he was enabled to add much information concerning the details of structure of the calciferous glands. His figures[4] and description of the transverse sections of the second and third pairs of glands and of the wall of the esophagus in the somites containing them furnish us the first successful attempt to make known the peculiar structure of that part of the alimentary tract. They established the presence of the longitudinal chambers or "follicles," and the separating lamellae which subdivide the space between the inner epithelium and the outer muscle layers of the esophageal wall. They also made known the presence of the series of longitudinal blood vessels which are distributed between the inner boundaries of the longitudinal chambers and the epithelial layer of the wall. The existence in the middle of each lamella of vascular connections between the outer and inner series of longitudinal blood vessels was also made known. The fact that what were termed second and third pairs of glands were merely lateral expansions of the glandular wall with which they were related was made clear for the first time.

Claparède believed that the anterior pair of glands was in somite 11, and that the so-called "second pair of glands" was close to them in the posterior part of the same somite, and that the third pair was in the 12th somite. Not only did he fail to correctly locate the glands, but he also failed to recognize the direct communication of the cavities of the three pairs of glands. He seems to have believed that the contents of the "follicles" or chambers of the posterior glands discharged their contents through small clefts of the epithelium into the lumen of the esophagus; and in a footnote, although he intimated the correctness of Leo's claim that there were no large openings for such passage, he claimed that Leo's opinion that the cavities of the three pairs were united was incorrect. "Diese Abwesenheit von grösseren Mündungen an den Blätterdrüsen war bereits dem Leo[5] aufgefallen. 'Orificia horum corpusculorum in oesophago

[4] Drawings from two of these figures have been reproduced as figures 8 and 9.

[5] In a footnote on page 617, Claparède discussed the failure of various investigators to recognize the important contribution of Leo to a correct understanding of the function and relations of the spermducts, and referred to a figure which was included in Leo's paper This figure has been copied and reproduced as figure 1 in the present paper, since it was the occasion of a very apt comment of Claparède which applies to Leo's noteworthy success in his study of the calciferous gland as well as of the spermducts. "Das Verdienst der ersten Entdeckung und genauen Erkenntniss gebührt nichtsdestoweniger dem jetzt ziemlich vergessenen Leo."

nunquam vidi' sagt er. Darauf setzt er hinzu: 'cum sacculis autem antecedentibus conjuncta mihi videbantur' (loc. cit. p. 14), was entschieden unrichtig ist." Two factors presumably contributed to his failure to find the passage-ways between the cavities of the second pair of glands and those of the first pair. The narrowed connecting passages are often somewhat tortuous, (depending perhaps on the degree of contraction of that region of the worm when killed), and are correspondingly difficult to follow in sections. Serial sections are almost essential for tracing them in many specimens, but the technique involved in the preparation of such sections was not developed until a considerably later date (1881). Claparède's failure to understand the structure and function of the first pair of glands is indicated by the following footnote on page 606: "Unmöglich ist es auch nicht, dass der Stoff zu den grossen Kalkconcrementen der vorderen Säcke ursprünglich von diesen Drüsen abstammt und durch eine Art Regurgitation bis in diese Säcke geleitet wird. Der Umstand, dass die Wand dieser Organe keine drüsige Structur, sondern blos die normalen Schichten, selbst flimmenndes Epithel bietet, würde zu Gunsten dieser Ansicht sprechen."

Perrier (1874) did not definitely state that the three pairs of "glandes du calcaire" are in the 10th, 11th, and 12th somites; but, he stated that they are in the same somites as the "testicules" (p. 351) and elsewhere (p. 367) located the testicules in somites 10, 11, and 12, therefore it seems probable that he was aware of the actual position. This is the earliest account known to the writer in which they are correctly located. He claimed that all three pairs of glands have fundamentally the same type of glandular structure, all having flattened glandular lamellae. In other respects, his anatomical account added nothing to that of Claparède, and was less accurate when he stated: "Ces feuillets sont placés entre la couche vasculaire et les couches musculeuses de la paroi oesophagienne." The importance of Leo's observations were apparently less obvious to Perrier than they were to Claparède.

Horst (1876) in a paper of about 30 pages with one double plate has given the results of his studies of the anatomy of *Lumbricus terrestris*. He described three pairs of calciferous glands, located in the 10th, 11th, and 12th somites. A figure which shows the relations of the principal blood vessels of the first dozen somites makes it obvious that Horst had a definite and correct conception of the location of the three pairs of glands and of the lateral "hearts" associated with them. He was no more satisfactory than Claparède in his discussion of the relations of the cavities of glands of one pair to those of others and to the lumen of the esophagus. He wrote of his inability to find the clefts in the epithelium through which Claparède supposed there was a communication of the cavities of the second and third pairs of glands with the esophageal lumen. Frequent references are made

to the papers of Lankester, Claparède and Perrier, in his discussions of both the anatomy and physiology of the glands.

Darwin (1881) devoted several pages to a discussion of the functions of the calciferous glands, but accepted Claparède's ideas concerning the relations of the glands to each other and to the esophageal lumen. The belief that there is no direct communication between the cavities of the first pair of glands and the chambers or "follicles" of the second and third pairs led to his misinterpretation of the narrow connecting passages affording such direct communication.

He commented on the slight amount of information contributed by Claparède concerning the structure of the first pair of glands, and on his assumption that the calcareous matter forming the concretions is derived from the other two pairs of glands. Darwin mentioned the presence of lamellae in the first pair of glands when they contain only small concretions and made the following statement. "After the formation and expulsion of a large concretion, new lamellae must be developed in some manner. In one section made by my son, the process had apparently commenced, although the gland contained two rather large concretions, for near the walls several cylindrical and oval pipes were intersected, which were lined with cellular matter and were quite filled with free calciferous cells. A great enlargement in one direction of several oval pipes would give rise to the lamellae." It seems to the writer altogether probable that these "pipes" were the narrowed connecting passages between the cavities of the first and second pairs of glands. As a result of a number of observations and considerable thought Darwin reached the conclusion: "With respect to the function of the calciferous glands, it is probable that they primarily serve as organs of excretion, and secondarily as an aid to digestion."

Vejdovský (1884) made but brief references to the calciferous glands of Lumbricidae and announced his intention to discuss them at greater length in a later publication in which not only the glands in Lumbricus but those in other locally distributed genera would receive attention. He gave the location of the glands in 10, 11, and 12.

Marshall and Hurst included the earthworm among the forms described in their Practical Zoology of which the first edition appeared in 1887. The writer has not seen a copy of the first edition, but, on the assumption that the principal features of the description of the calciferous glands agreed with those in later editions, they seem to have been the first workers since Henle (1835) to confirm some of the more important observations of Leo (1820). They described the second and third pairs of glands as communicating with the first pair which open directly into the lumen of the esophagus. The description of the structure of the second and third pairs of glands agrees in the main with that of Claparède (1869). They located the first pair of glands in 10, as had Perrier (1874), Horst (1876) and Vejdovský (1884).

Kulagin (1888) contributed brief notes on several topics connected with earthworm anatomy, some of which dealt with the calciferous glands. He referred especially to *Lumbricus rubellus*, "*Allolobophora mucosa*" (=*Helodrilus roseus*),[6] and *Allolobophora* (=*Helodrilus*) *foetida*. He mentioned the first pair as "Falte des Oesophagus von der rechten und linken Seite," divided internally, and with openings into the oesophagus always distinct. He referred to the communication between glands of the second and third pairs where they are in contact as something not previously announced. He wrote of the second and third pairs of glands of *H. roseus* as not lying on the right and left sides of the esophagus, but, as surrounding it. This is the earliest definite statement noticed by the writer concerning a type of calciferous gland anatomy which in more recent times has been found to be of very frequent occurrence.

Rosa contributed quite a large number of papers in which are found descriptions of various species of Lumbricidae. Brief statements concerning the calciferous glands are found in a considerable number of these descriptions. The writer has not noticed any detailed account, in any of Rosa's papers, of the internal structure or relations of these glands, but statements concerning the number of pairs of glands, their superficial appearance, and the location of the somite or somites containing them occur frequently. In at least two of them (1887 and 1893, p. 15) attention was called to differences in the number of glands present in different species; three pairs in *Lumbricus herculeus*, in 10, 11, and 12; but one pair, in 10, in a considerable number of species. In one paper (1895), he described a species having one pair of glands, in 9; another with but one pair of glands, in 10; another with but one pair of glands, in 11; while in still another one (*Allolobophora robusta*) they are not superficially recognizable. Rosa in his recognition of the number and location of the calciferous glands as useful characters in distinguishing species of Lumbricidae was later followed by Cognetti.

Beddard (1895) gave an extended account of the various types of calciferous glands found in the different families of earthworms. Those of Lumbricidae were discussed but briefly. Claparède is mentioned as having studied the minute structure of the glands in Lumbricus. Marshall and Hurst were given credit for being the first to correctly locate the first pair of glands in 10, and also the first to correctly describe the relation between

[6] The genus name Helodrilus Hoffmeister was adopted by Michaelsen (1900a) as the technically correct name for a group of Lumbricidae which had for a considerable number of years been known under the genus name Allolobophora Eisen. The change in name was assumed to be necessary for strict conformity with requirements of certain accepted rules of nomenclature. Most systematists in this group followed his example. In recent years Michaelsen and some others have returned to the use of the name Allolobophora. The writer knows of no authoritative decision that Helodrilus is not the technically correct name and hence it is used in this paper.

the cavities of the three pairs of glands with each other and with the lumen of the esophagus. As has already been stated, credit for the first announcement of these facts belongs to others.

Moore (1895), in the description of "*Bimastos palustris*," an interesting species of Lumbricidae from the vicinity of Philadelphia, Pennsylvania, compared the structure of the calciferous glands with those of *Lumbricus terrestris*, as described by Claparède. He found that the modified part of the esophageal wall with its tunnellike chambers and separating lamellae extended to the 14th somite, although the width of the lamellae and chambers was considerably less in this region. This is the earliest account noticed by the writer in which the posterior end of the calciferous gland structure has been correctly located. A further discussion of Moore's paper will be found on a subsequent page in connection with a statement of the results of a study of specimens of this species by the writer.

Harrington (1899) gave the most complete and in some respects the most accurate account of the Lumbricid type of calciferous gland that appeared in the 19th century. His studies were based on the glands of *Lumbricus terrestris* and his treatment of the anatomy and histology was but a foundation for his presentation of the results of his studies of the physiology of the calciferous glands. The author died without having revised the proofs of his paper and some errors, to be discussed later, might otherwise have been eliminated. He listed the paper of Leo and made two brief references to his work, but apparently was not aware of the more important discoveries announced by that investigator. "Since Julius Leo, in 1820, discovered lime-secreting organs leading into the digestive tract of earthworms, very many workers have examined and reported observations upon these interesting structures." "Julius Leo ('20), who first described the calciferous glands, says concerning them: 'Qui usus corpusculorum fugit me.'" This quotation from Leo is also contained in a footnote in the paper of Claparède. Harrington credited to Morren the suggestion that the glands might furnish lime for the egg capsule. This suggestion was made by Lankester (1894, p. 266). Lankester was credited with observing "that the calciferous glands opened into the alimentary tract," although Lankester stated that he found no such openings. Mention is made of some of these errors because they seem to account for errors in certain statements of a more recent writer. Certain errors in the list of literature will receive later attention.

Harrington announced two discoveries that involved important changes in the ideas of the structure of the glands. "The cavities are also continuous from somite X to XIV, opening at the former into the hollows of the first pair of glands, and at the latter directly into the oesophagus." (p. 108-109). The same idea is advanced in another place (p. 111-112). "If it (lime) is passed backward, it breaks through oesophageal epithelium, in

this case opening directly into the digestive tract at the middle of XIV. This second outlet for the secreted product has escaped the notice of previous writers." This assertion of the presence of normal posterior openings for the gland is adopted by one later writer (Combault, 1909) and disputed by Stephenson and Prashad (1919). The present writer is not convinced that such openings are normally present.

The second announced discovery mentioned above is outlined as follows: "The anterior pair of pouch-like glands are the only ones lined with true epithelium and are developed as diverticula of the oesophagus, while the two posterior pair are formed by migration of the amoeboid endodermal nuclei, which arrange themselves about cavities formed *de novo* near the splanchnopleure and give rise to the secretory elements." (p. 137).

"The unusual relations between the glandular and circulatory systems can be interpreted only by regarding the one-layered secretory lamellae bounding the blood spaces as greatly hypertrophied vascular walls representing both the intima and endothelium." (p. 106). This idea also is adopted in part by Combault and is repudiated by Stephenson and Prashad. In view of some recently ascertained facts to be discussed subsequently in this paper the writer believes that it is erroneous.

The major part of the paper is devoted to discussions and descriptions of the histology, physiology, and blood supply of the glands, which are subjects not included in the scope of this paper.

Ribaucourt (1901) published a paper of about 100 pages dealing with the comparative anatomy of the Lumbricidae and based especially on European representatives which were studied by modern histological methods. The "Glandes de Morren" received attention to the extent of about ten pages and some sixteen figures, based on studies of the glands of nine or ten different species representing several genera. The work had been carried on simultaneously with that of Harrington, but apparently neither knew of the work of the other. Ribaucourt called attention to the tendency of previous writers to assume that the glands of Lumbricus, which were the ones most studied, were representative of those belonging to worms of other genera, "ce qui est une erreur." No attempt was made to compare the results of his studies on the glands with those announced by previous workers. He simply described the glands of Lumbricus as he saw them, and then the glands of nine other species were compared with them, with especial attention to differences. Diagrammatic figures of longitudinal frontal sections of the glands of nine species were given, and these include representatives of six different genera of Lumbricidae which he recognized. Some of these genera are usually treated by systematists of the present time as subgenera.

Ribaucourt made no reference to the precise location of the glands and but little is stated about the relations at the posterior end. Some of his

plate figures indicate that the anterior end is in 10. In his discussion of the glands in Lumbricus, he went one step farther than Claparède or Harrington by his treatment of the series of longitudinal chambers in the wall of the esophagus, extending between the anterior pair of glands and the crop, as a distinct unpaired gland which he called "la glande antéro-postérieure," and designated as IV. He considered this to be the more primitive member of the series of glands and that the three pairs commonly recognized were secondary differentiations from it. "La glande antéro-postérieure de Morren est la plus ancienne, l'antérieure et les deux moyennes II, III n'en sont que des différenciations secondaires." As a result of his comparative studies of the glands of various species representing different genera of Lumbricidae, he found that the most simple form of gland development in the forms examined was that of *Helodrilus hermanni* in which only the gland IV was present. There were no paired anterior pouches nor paired expansions in next following somites. (This species is considered by Michaelsen (1900a), who originally described it, to be a synonym of *H. oculatus*.) Between the type of calciferous gland development in this species and that of *Lumbricus terrestris* occurred various intermediate degrees of complexity. Absence of the lateral expansions, designated by Ribaucourt as II and III, was especially common.

Combault published several brief papers in 1907, in which various topics related to the structure and physiology of the "glandes calcifères des Lombrics" were discussed. Since a more extended article by him (1909) presented in a more complete and unified form the results of his studies of these organs, attention will be given only to the contents of that paper. "Contribution a l'étude de la respiration et de la circulation des Lombriciens" is the title, and was the natural outcome of the author's opinion that the "glandes de Morren," as the glands are called in this paper, function chiefly as organs of respiration. The third division of the paper (pp. 24-35) entitled "Anatomie des glandes de Morren" contained the matter which will receive chief attention here. His historical account contained allusions to the earlier writers, which were obviously based on Harrington's statements and repeated the errors made by that writer. Leo is mentioned as the first to call attention to calciferous glands. His inability to ascertain their function was announced, but there was no mention of his important discoveries pertaining to the relations of the glands to each other and to the esophagus. Credit for these discoveries was given to later writers.

Combault gave Lankester credit for first describing the openings of the anterior pair of glands into the esophagus, and Claparède was mentioned as confirming that result. Leo first described and figured such openings. Lankester expressly stated that he did not find them, and Claparède quoted the statements of Leo in which they are mentioned. It is obvious

that the paper of Claparède received little or no attention from Combault, since he made a statement implying that Lankester alone, of the various investigators who published before Harrington and Ribaucourt, used modern methods. All others depended on dissections. Such a statement would be highly improbable from any one who had seen Claparède's detailed account of the various methods of fixation, staining, clearing, and mounting of sections; and who had examined the half dozen plates which illustrate the paper, and of which the majority of the figures were based on sections.

Combault described and figured the glands as located in somites 11 to 14, instead of having the anterior part or pair in 10. When the lateral "hearts" were figured they were represented in the correct relation to the glands since the posterior two pairs of hearts were shown associated with the anterior two pairs of glands. He agreed with Harrington in claiming that there are paired openings into the esophagus at each end of the gland region, even though admitting that such openings were not recognizable in 14. About the only real contribution or advance in our ideas of the anatomical relations of the calciferous gland structures, made by Combault, is the suggestion that the glandular region in the posterior part of the esophagus in Lumbricidae should be considered as one gland instead of several pairs of glands. The major part of the paper is given to discussions of the histological and physiological features of the glands and has been reviewed by Stephenson and Prashad (1919). The bibliography contained nearly 200 titles, some of which included errors that had occurred in the lists of previous writers and presumably were incorporated without checking for determination of correctness. Harrington listed a paper: '42 Henle, F. G. J. Müllers Archiv. pp. 238-280, 1842. The paper was really by Dr. Friedrich Stein. Precisely the same reference occurs in the list of Combault. A typographic error in the reference to the paper of Perrier (1874) in the literature list of Vejdovský (1884), which indicated the pages as 331-350 instead of 331-530, was reproduced in Harrington's list and again in that of Combault.

In a paper which was published in 1917, the writer included in the brief summary of distinguishing characters of each of about a dozen species of Lumbricidae the approximate number of the lamellae separating the gland chambers. The expression "longitudinal partitions" was used and reference was made to "the calciferous gland." The number of the partitions was necessarily approximate, since there is some variation in the number in different parts of the same organ as well as individual variation. These numbers are perhaps not very significant except where there is a considerable divergence. It seems improbable that such numbers as 40 and 60 would be found in different adult individuals of the same species unless represented by different varieties.

Stephenson and Prashad (1919) contributed an article on the calciferous glands of earthworms which dealt with these organs in representatives of three different subfamilies of Megascolecidae and of two genera of Lumbricidae. The discussion of the last named family included descriptions of the structure of the glands in young and adult *Helodrilus caliginosus;* in *H. parvus*; and in a species of Lumbricus, presumably *L. terrestris*. The morphology of the glands, including the histology and general anatomy, received chief attention; and there was an extended review of papers of Harrington and Combault in which their peculiar views and statements concerning the histology and physiology of the glands were carefully discussed. The authors presented evidence and arguments in support of their contention that the complex type of gland found in the Lumbricidae has had its origin in a more simple type of gland. "The condition in the Lumbricidae originated in a series of longitudinal lamellae. The mode of evolution has been comparable to what has happened in *Eutyphaeus*—the inner edges of the lamellae have fused. In this way a series of longitudinal tunnels has been formed, in and part of the epithelial coat of the oesophagus, and entirely within the muscular coat. These tunnels open in front, where the longitudinal folds begin, into the oesophageal pouches in segment X; they become progressively smaller, and cease in XIV without posterior openings.

"The epithelium of the glands is in all cases continuous with that of the oesophagus, and comparative anatomy shows that the various forms of glands are essentially due to various forms and degrees of complexity of the epithelial folds. The glands are therefore not mesodermal in origin, and are not merely the walls of blood-vessels, as has recently been contended."

They agreed with the suggestion of Combault that the gland should be considered as a single organ rather than as several pairs of glands. In the historical résumé of the contributions of earlier works on the calciferous glands, they began with that of Lankester who was credited with being "the first to examine them in any detail, though Morren had given a rough figure without any accurate description." The papers of Leo (1820) and Henle (1835) were not mentioned. Some of the better known text-books received attention and Marshall and Hurst were credited with being the first to correctly give the location of the glands. Their description was outlined without adverse comment other than that implied in the general statement applying to all of the text-books mentioned: "We do not think that a student would arrive at an adequate conception of the glands from any of these descriptions."

An examination of about 45 different high school and college text-books in which the calciferous glands are discussed and which are in use in the United States, or have been within recent years, has made it very evident

that in the majority of cases the writers have relied chiefly on the statements and illustrations found in previously existing text-books, as a basis for their own statements and descriptions. Certainly the majority of the authors could not have examined with any care a series of sections through that part of the esophagus located in the somites 10-14, or have very closely studied a careful dissection of that part of the esophagus in *Lumbricus terrestris*, which most of them obviously attempt to describe. The least faulty descriptions are usually those of which the ancestry can be traced back to the Marshall and Hurst text-book. But one of the authors (Hegner) gives evidence of familiarity with the paper of Harrington, which appeared in a well known and much used American journal. There may be ample justification for omitting any account of the calciferous glands from our text-books, but there seems to be no valid excuse for statements that are contrary to facts. Statements like one which appeared in a recently published American text-book are more than a half century behind the times, since they have less that is true and more that is untrue than is found in the combined accounts of the calciferous glands, by Claparède in 1869 and Leo in 1820. The statement to which reference is made is as follows: "The oesophagus begins at the posterior end of the pharynx in the region of the sixth segment and continues posteriorly as a thin-walled, undifferentiated tube to the fourteenth segment, where it connects with the crop and gizzard. Three pairs of calciferous glands open into the oesophagus near its posterior end." The part of the esophagus which is in somites 10-14 is not a thin-walled, undifferentiated tube. The calciferous gland development is in the esophageal wall and included between the epithelial layer, which surrounds the lumen, and the muscular layers which form a part of the wall. In the absence of any statement to the contrary, the natural implication would be that the glands of the three pairs open in a similar manner into the esophagus, which is not true. The esophagus certainly does not connect with the gizzard at the "fourteenth segment."

The text-book description criticized above is by no means unique. It illustrates a kind of treatment of the subject that is to be found in a considerable number of those in common use. Most of the authors have exhibited a tendency to depend too much on statements found in other text-books.

A brief résumé of the various discoveries leading up to our present day knowledge of the calciferous glands of the Lumbricidae may be stated, in approximate chronological order, in the following manner: In *Lumbricus terrestris*, the posterior part of the esophagus has three pairs of glands. Those of the anterior pair are saclike in nature and their cavities communicate with the lumen of the esophagus through paired oblong openings in the lateral walls of the esophagus, one such opening for each of the two glands.

The other two pairs form a sort of cylinder containing longitudinal folds or lamellae which are radially arranged. No openings from these two pairs of glands leading directly into the esophageal lumen were found, but they seemed to communicate with the anterior pair. Leo in 1820 gave us this much of a start. Lankester in 1864 showed that there is a conspicuous series of parallel longitudinal blood vessels related to the outer surface of these glands. Claparède in 1869 made known a similar series of parallel longitudinal blood vessels related to the inner layer of the gland formation. He also furnished a much more definite idea of the nature of the longitudinal lamellae which separated the longitudinal chambers or follicles in the second and third pairs of glands, and showed that the middle or vascular layer of the lamellae furnished vascular communications between the two series of longitudinal blood vessels already mentioned. He made clear for the first time that what are termed the second and third pairs of glands are lateral expansions of the glandular esophageal wall with which they are related.

Perrier in 1874 announced that the first pair of glands contained flattened glandular lamellae like those of the other two pairs. He did not definitely state which somites contained the glands but from what he did state we are led to infer that they are in somites 10, 11, and 12. This was the first account furnishing data for their correct location. Horst in 1876 definitely located the glands in 10, 11, and 12. Statements and figures alike give that location. Marshall and Hurst in 1887 in their Practical Zoology confirm the opinion of Leo, that the cavities of the second and third pairs of glands communicate with those of the first pair and through them with the esophageal lumen. It took two thirds of a century to get this opinion of Leo definitely established.

Moore in 1895 definitely determined the posterior end of the calciferous glandular formation in one species of Lumbricidae in the 14th somite; but the earliest definite statement correctly locating the posterior end of the gland in *Lumbricus terrestris*, that has been noticed by the writer, is that of Harrington in 1899 who also found it to be in somite 14 in that species.

Combault in 1909 made the suggestion that instead of three pairs of glands, it is more reasonable to consider that we are really dealing with a single calciferous gland.

Stephenson and Prashad in 1919 presented arguments in support of a claim that the calciferous gland has had its origin in a glandular development involving the formation of a series of longitudinal folds of the lining epithelium of which the inner or free margins have fused, giving rise to a series of tunnellike chambers included between the muscular layer of the esophageal wall, and the epithelial layer, which surrounds the lumen of the esophagus.

An interesting parallel to such a supposed series of intermediate stages culminating in the complex organ present in modern Lumbricidae is found

in the calciferous glands of various species of Diplocardia. They are described in another part of this article.

Rosa, first in 1887, and subsequently in other papers, mentioned several species in which there is but one pair of calciferous glands, those being located in the tenth somite. Kulagin in 1888 stated that in one species the second and third pairs were not laterally placed but surrounded the esophagus.

Ribaucourt in 1901 described the calciferous glands in a considerable number of different lumbricid species showing much variation in the appearance of the glands. One of them was assumed to be of an ancestral type, since it showed no lateral enlargements of the glandular wall.

TYPES OF CALCIFEROUS GLANDS IN LUMBRICIDAE

The more important general facts of the anatomy and of the relations of the cavities in the different parts of the gland to each other and to the esophageal lumen have already received attention. We have now to consider some of the various types of glands found in different species of Lumbricidae. As has already been pointed out by different writers, the essential feature of the gland is the series of longitudinal chambers contained in the esophageal wall of several somites and ordinarily terminating anteriorly in 10 and posteriorly in 14. These chambers and the lamellae by which they are bounded occupy the greater part of the space produced by the separation of the inner epithelial layer of the esophageal wall from the muscle layers in the outer part of the wall. The so-called vascular layer normally included between the epithelial and muscle layers of the esophageal wall is very intimately associated with the walls of the gland chambers being represented in the longitudinal blood vessels extending along the outer and inner margins of the chambers, and in the vascular middle layer of the separating lamellae. These chambers are continuous throughout the length of the gland; they apparently end blindly in 14 without normal openings into the esophageal lumen; and they usually open anteriorly in 10 into cavities continuous with the lumen. The anterior openings may be into cavities of relatively large evaginated pouches occupying a great deal of space in 10, or the cavities may be insignificant and but slightly differentiated from the lumen. In two species, at least, the anterior openings are in 11, instead of in 10. There may or may not be lateral expansions of the gland in one or both of somites 11 and 12.

The ease or difficulty of a study of the glands is dependent on several different factors. Important among these is the state of contraction existing in the anterior part of the specimen at the time of fixation. The state of preservation is important, especially when one is attempting to determine the presence or absence of posterior openings of the gland chambers. The general plan of structure is an important factor in an attempt to demonstrate the continuity of the chamber cavities in the anterior part of the gland with cavities that are connected with the esophageal lumen. In specimens of some species in which the outer part of the gland wall is nearly cylindrical in the two or three anterior somites and without noticeable constrictions where the septa are attached, such continuity may be obvious in a single sagittal section (Fig. 50). In other specimens with a type of gland in which the diameter of the gland at 10/11 is much less than

in the part lying anterior to the septum, an examination of a considerable number of consecutive sections is sometimes necessary before such continuity can be determined.

Figures of longitudinal sections of the glands have been prepared in most cases from sections cut in the frontal plane, since the esophageal pouches and characteristic enlargements of the gland in some species are chiefly lateral in position and hence are shown to the best advantage in such sections. Because of the unavoidable irregularities in the position of the various parts of such a long organ of complicated structure, in specimens often more or less contracted and contorted, the frontal sections that show the characters to the best advantage for one part of the organ are almost certain to be unsatisfactory for some of the other parts. Sections necessarily pass obliquely through the wall chambers and lamellae in some parts of the organ and often in most parts. Diagrammatic figures like those of Ribaucourt and Combault are so unsatisfactory that it was decided to use for this paper camera drawings from sections, in the belief that they would be at least as useful and more accurate. Not infrequently the histological condition of the only specimens available for sectioning has been unsatisfactory.

ESOPHAGEAL POUCHES WANTING

The species first considered are those in which there is an absence of paired lateral evaginations of the esophageal wall in somite 10. They lack the paired esophageal pouches, called by Ribaucourt and Combault "diverticules de Perrier," and often designated as the "first pair of glands." The simplest form of glands of this type in the Lumbricidae known to the writer is found in *Helodrilus oculatus*, a European species, and will be the first to receive attention. The glands of three other species included in this group have been studied and will be described. These species are *Helodrilus venetus* and the variety *H. v. hortensis*, *H. foetidus*, and *H. lönnbergi*.

Helodrilus oculatus Hoffmeister. Ribaucourt (1901), as previously noted (page 18), gave a brief description of the gland in this species, using a former name, *Allolobophora hermanni*. The writer is fortunate in having two specimens which were collected in Europe, and identified and presented to him by Dr. Michaelsen, some years ago. Transverse sections of the anterior end of one of these specimens make possible certain additions to the description by Ribaucourt. This is desirable since that writer assumed that the gland is of a more primitive type than are those of the other species examined by him. The anterior end of the gland is in somite 10, approximately midway between 9/10 and 10/11, and the posterior end is in somite 14. There is but little variation in the diameter of the esophagus or of its lumen in the different parts of the gland region, and in the esophageal somites next anterior to it. There are no lateral evaginations

in 10 at the anterior end of the gland comparable to the "esophageal pouches" found in most Lumbricidae. Unpaired irregularities like those shown in Ribaucourt's figure (1901, Fig. 23) are not very obvious and when present may perhaps be temporary and due to a contraction of that part of the body of the worm.

The inner epithelial layer forms numerous short elevations or papillae in the anterior part of 10 (Fig. 11) and in the preceding somites, but in the gland forms a few low longitudinal ridges and shallow grooves. The character of the epithelium differs somewhat in the gland region where the surface has numerous short, fine, parallel processes projecting into the lumen. It is the type of epithelium described by Stephenson and Prashad (1919) and by them called rodlet epithelium.

As one follows a series of sections posteriad, beginning at the anterior end of the gland, the longitudinal chambers of the lateral walls are the first to appear (fig. 10), soon followed by those of the dorsal and ventral sides. The number of the chambers and their relative magnitudes, as seen in transverse section, are shown in figures 12 and 13. The openings of the chambers into the lumen at the anterior end of the gland are traced with difficulty and none are conspicuous. There is no appreciable change in the dimensions of the chambers where the septa connect with the esophagus, but there is a gradual decrease in the width of the chambers between the lamellae and a relative increase in the thickness of the lamellae, as one follows the series of sections posteriad (Fig. 14). This change in thickness is due, at least in part, to an increased amount of blood in the median vascular layer of the lamellae. A careful search has not led to the discovery of any communication between the posterior ends of the longitudinal chambers and the lumen of the esophagus. This was the simplest type of gland described by Ribaucourt and found by him in but one species. Rosa (1895), in his description of *Helodrilus robustus*, writes of the calciferous glands in a way that seems to indicate a similar type of gland in that species. "Le ghiandole di Morren non sono esternamente reconoscibili."

Helodrilus venetus var. *hortensis* (Michaelsen) is a widely distributed earthworm type, well known in Europe, and recorded from Asia, Africa, and both American continents. The only record from the United States, noticed by the writer, is by Michaelsen (1900) and was based on specimens from California. During the past two years more than three hundred specimens which are assumed to belong to this variety have been collected from the banks of a stream flowing through Urbana, Illinois. Serial sections of anterior parts of ten specimens have been examined as a basis for the statements concerning the calciferous gland of this form. Two of the series are sagittal; four, transverse; and four are frontal.

The calciferous gland of this form resembles that of *H. oculatus*, in the absence of evaginated pouches in 10, and in lacking any definite inflations

in any one or more of the following somites. It more nearly resembles the glands of most other species in the general proportions of the chambers as shown in transverse sections (Fig. 17). The position of the anterior end of the gland is somewhat variable, but is in somite 11 in all of the specimens studied. In most of the specimens it is very near the anterior end of the somite, being but slightly posterior to the place of union of the septum 10/11 with the wall of the esophagus. In one specimen it is about midway of the somite and in another one is about one-third of the length of the somite from the anterior margin. These statements are made with the assumption that the part of the esophagus included between the septa 10/11 and 11/12 belongs to somite 11.

In *H. v. hortensis* the anterior ends of the lamellae have their inner margins free for a very short distance and two or more of them may be included in a single subepithelial cavity (Fig. 16) which opens through a single channel into the esophageal lumen. Although there are approximately 40 of the wall chambers, there may be less than half of that number of the channels opening into the lumen. The course of these channels may be at right angles to the long axes of the related chambers or may even be directed somewhat posteriad as they approach the lumen (Fig. 15). 38, 40, 40, and 43 are the numbers of wall chambers present in the glands of the four specimens of which transverse sections were made, as shown in sections near 11/12 in each. The width of the chambers in the plane parallel to the separating lamellae is somewhat greater in the anterior two or three somites of the gland than in the posterior ones, but the difference is not very marked. No communication of the cavities of the chambers at their posterior ends with the lumen of the esophagus has been found.

Helodrilus venetus (Rosa) in its typical form is well known in Europe and Asia. Three European specimens collected at Trieste were identified by Dr. W. Michaelsen and kindly presented to the writer a few years ago. Two of these have been sectioned in part and have given an opportunity for a comparison of the characters of the gland found in *H. v. hortensis* with that of the typical form of the species. The chief difference noted is in the number of wall chambers (Fig. 19), which is 61 in the single specimen of *H. venetus* typ. of which transverse sections were made, instead of approximately 40, as in *H. v. hortensis*. The anterior end of the gland in *H. venetus* is approximately midway of somite 10, instead of being in 11, as in the variety *hortensis*. The specimens of *H. venetus* were very strongly contracted and the glands correspondingly shortened and somewhat contorted. This fact probably accounts for the apparent inflations of the gland wall between the septa of its anterior somites. In the structural characters of the glands of the two forms, there is a marked similarity (Fig. 18).

Helodrilus foetidus (Savigny) is a very abundant and widely distributed species and has a gland that is similar in some respects to that of *H. v. hor-*

tensis. The anterior end of the gland is in somite 11 instead of 10 and is without paired evaginated pouches. Figures 20 and 23 show the chambers to be relatively narrow in 11; in 12 they are very much wider in the lateral walls (Fig. 20 and 24); and posterior to 12 they are again narrow, as in other species. Ribaucourt's description and figure 28 represent the general form correctly and his figure 63 shows the anterior end of the gland associated with the posterior pair of hearts indicating the 11th somite. Combault's figure represents the anterior end as relatively much larger than it really is, and his description places it in the same somite as he gives for the anterior end of the gland in other species, viz., in somite 11. This position happens to be correct for *H. foetidus* but incorrect for most others.

A study of transverse sections shows that the cavities of two or more chambers may be in communication with the esophageal lumen through one connecting channel (Fig. 21 and 22), as in *H. venetus hortensis*, but there is no corresponding display of free inner edges of lamellae grouped in subepithelial cavities like those found in that form (Fig. 16). The number of wall chambers is approximately 60.

Helodrilus lönnbergi (Michaelsen) was described in 1894 from specimens collected at Savannah, Georgia, and was later recorded from North Carolina (Michaelsen, 1900). The first specimens seen by the writer were immature individuals which were sent from the U. S. National Museum for identification. They had been collected by Dr. E. T. Wherry in an acid bog near Riverdale, Maryland, while he was carrying on certain investigations on acid soils. No clitellum was present and positive identification could not be made; hence an appeal was made to Dr. Wherry for more specimens to be obtained in the Spring. He accordingly collected additional specimens on March 9, 1924 and shipped them in living condition. Some of them were at the height of sexual activity and furnish the basis for much of the following description of the calciferous glands. Michaelsen had noticed the conspicuous enlargements of the esophagus in somites 11 and 12 and that they were of the nature of calciferous glands.

Transverse and longitudinal sections have shown that the gland of this species is fundamentally like those of other Lumbricidae, but it has superficial differences in general form that are conspicuous. The lateral enlargements of the esophagus in 11 and 12 in immature specimens occupy the greater part of the space in those somites and are due to the great width of the chambers and their separating lamellae (Fig. 82). The glandular development extends into 10, but the chambers in that somite are relatively narrow and there are no evaginations of the wall to form "pouches." The openings of the chambers into the lumen are very obvious and are illustrated in figures 25 and 27. In the latter (Fig. 27) which is slightly oblique, the right hand part of the figure represents a part of the section just at the anterior end of the chambers, while the left hand part of the

figure is from a part of the section which is a little posterior to the chamber ends. On the right, the ends of the cavities of two chambers are shown communicating through a single short channel with the lumen. A similar relation is shown for the two chambers next above, but not quite so clearly, because the posterior wall of that short channel is included in the section. Other such communications are shown in other sections, and in one instance the ends of four chambers open through the same short channel. In somites 13 and 14 (Fig. 26) the gland is of small diameter and the chambers are relatively narrow. No evidence of any posterior communication of the chambers with the esophageal lumen has been found after careful search.

The gland contained much calcareous material in some sectioned specimens and similar contents were conspicuous in others that were dissected. A peculiar histological condition of the separating lamellae is obvious in most of the sectioned specimens and an attempt has been made to represent this in figure 29 which is from a section through the anterior part of a region where secretion had been active at the time that the specimen was fixed. A noticeable shreddy or feathery appearance is presented by the parts of the lamellae nearer to the outer muscular layer. The parts of the lamellae nearer to the inner epithelial layer have a quite different and more normal appearance.

The species thus far described, except *H. oculatus*, are often assigned to a subgenus Eisenia which is characterized by the position of the spermathecal pores near the median dorsal line. One other species of this subgenus which is common in North America and available for study is *H. roseus*. The calciferous gland of this species more closely resembles those of the group of species of which a description and discussion next follow.

ESOPHAGEAL POUCHES PRESENT; NO OTHER LATERAL ENLARGEMENTS

The other groups of species to be considered include those in which the anterior part of the calciferous gland has a pair of lateral evaginations of the esophageal wall, including cavities with which the wall chambers are in communication. This includes a majority of the species of Lumbricidae of which the glands have been studied. The species to first receive attention will be those in which there are no conspicuous definite lateral expansions of the gland wall posterior to the esophageal pouches, which is the term by which the evaginations will be designated.

Helodrilus palustris is an interesting North American species described quite fully by Moore (1895). He gave a detailed account of the calciferous gland and several excellent figures illustrating its anatomy. Dr. Moore kindly presented the writer with a few specimens several years ago, and these have furnished an opportunity to supply certain facts in addition to those found in his description. Moore noted the uniformity in diameter

of this part of the esophagus, and the lack of pouches which are so conspicuous in Lumbricus, and which account for the custom of using the plural term "glands" in referring to it. His diagrammatic figure of a median sagittal section represents the anterior end of the gland as near the middle of somite 10, but his description implies that it is in the 11th somite. Figures 30 and 31 are from series of longitudinal sections of the writer's specimens and show clearly that the gland begins in 10. The epithelial layer is described as ciliated, but the figures of Moore and the writer's sections indicate that it is an example of "rodlet epithelium." At the anterior end of the gland there is an abrupt, definite, lateral expansion of the esophageal wall on each side of the esophagus and accompanying lateral extensions of the esophageal lumen forming cavities which are narrow antero-posteriorly, but more extensive laterally. These cavities communicate directly with the esophageal lumen and into them open the channels through which direct communication of these cavities with those of the wall chambers is established. They correspond in essentials with the cavities of the esophageal pouches or "first pair of glands" of such species as *Lumbricus terrestris* and will be considered as their equivalents, though relatively small in extent. The lamellae of the lateral walls are much wider than those of the dorsal and ventral walls and the esophageal lumen is reduced to a cleft posterior to the pouches, although the outer wall, as seen in transverse sections, is approximately circular in outline. Moore stated that he had not "found the rifts, or communications, between the follicles and the esophageal lumen, which Claparède observed in Lumbricus." Moore makes no reference to communications at the anterior end of the gland between the follicles (wall chambers) and the lumen and presumably thought that there were none. The writer's sections show narrow tubular channels lined with cilia and connecting the anterior ends of several of the chambers with the cavities at the anterior end of the gland, which open into the esophageal lumen. One such connecting tube is represented in figures 31 and 32. No communications have been found at the posterior end. There is a definite increase in the diameter of the gland over that of the esophagus, as shown in figure 30, and the chambers are much more narrowly wedge-shaped than are those of *H. oculatus*, but nevertheless the gland in *H. palustris* is an interesting intermediate type between that of the former species and certain more highly differentiated ones to be described later.

Helodrilus gieseleri (Ude) was originally described from specimens collected in Florida and the variety *H. g. hempeli* Smith from specimens collected in Illinois. The anatomy of the calciferous glands in these forms is very similar to that which is found in several closely related species belonging to the North American group of earthworms for which Michaelsen (1900a) established the subgenus Bimastus.

The gland has paired esophageal pouches in 10 but no special paired enlargements in 11 and 12 (Fig. 33). The chambers and separating lamellae, characteristic of the gland wall in somites posterior to 10, extend forward into the posterior part of the pouches in 10, and the lamellae are continued still farther forward as folds which are united at their base with the outer walls of the pouches, but with their inner margins disconnected and projecting freely into the pouch cavities (Fig. 34). Figure 35 is from a section slightly posterior and 36 from a section still farther posterior to the one figured in 34. They show that communication of the cavities of the wall chambers with the pouch cavities is afforded through openings arranged in a series along the outer wall of the pouches and ranging from the dorsal to the ventral parts of the same. The differences in relations shown in the two pouches is due in part to the sections being somewhat oblique, and perhaps in part to differences in the state of contraction, or of pressure of the surrounding organs. Figure 37 is from a sagittal section through the anterior end of the gland and near the lateral wall. It shows clearly the communications between the pouch and chamber cavities. Figure 38 is from a similar section of a specimen of the variety ***hempeli***; the other figures being from a specimen of the typical form of the species. The chambers are approximately 40 in number and extend into somite 14 where they are much narrower than in the more anterior somites.

Helodrilus beddardi (Michaelsen) is another species originally described from North American specimens and found to range over a considerable part of the continent. It has also been reported from Asia by Michaelsen (1910) who has expressed doubt concerning its being specifically distinct from *H. parvus*. The general characters of the calciferous gland conform with those already described in *H. gieseleri*; definite esophageal pouches in 10; the lamellae and wall chambers wider in the anterior somites of the gland, but without definite conspicuous expansions like those of *Lumbricus terrestris* (Fig. 39). The number of wall chambers is approximately 40 throughout the major part of the gland. Figure 40 is from a transverse section through the pouches at the anterior end of the gland in a specimen collected in an acid bog. The lamellae folds are relatively wider than in ordinary specimens.

Helodrilus parvus (Eisen). This species was described from specimens collected in North America over which continent it is widely distributed. It has also been recorded in Africa and in different parts of Asia. The calciferous gland of this species was described in detail by Stephenson and Prashad (1919) with a figure from a transverse section through the esophageal pouches in 10.

Several series of sections from specimens collected in different parts of the United States have been available for study and an examination shows general conformity of the gland characters with those described in

this species by Stephenson and Prashad and with those described above in the species *H. gieseleri*. The chambers and separating lamellae, characteristic of the wall of the gland in somites posterior to 10, are continued forward into the posterior part of that somite and the lamellae are continued still farther forward as folds which are united at their base with the outer walls of the esophageal pouches, but with the other margins of the lamellae disconnected, and projecting freely into the pouch cavities. Figure 44 is from a frontal section of a specimen of this species and shows two features that deserve mention. The dilation of the lumen in somite 13 is due to the lodgment at that spot of a mass of food material at the time the specimen was killed. The esophageal pouches present an appearance which is duplicated in one other specimen of which sections were examined. The pouches are more commonly dilated and saclike, extending farther out into the coelomic space.

Helodrilus roseus (Savigny) is a species which is widely distributed and found in all the continents and in most regions where Europeans have settled. The calciferous gland of this species was figured and described by both Ribaucourt and Combault. The latter author erred in the position of the anterior end of the gland and in the number of somites involved. A pair of esophageal pouches in 10 very definitely determine the position of the anterior end of the gland. There are no definite lateral expansions of the gland wall in somites posterior to 10 comparable to those in *Lumbricus terrestris* (Fig. 54) or in *Helodrilus lönnbergi*. The wall chambers and separating lamellae are continued into the posterior half of the esophageal pouches and there the cavities of the pouches and of the chambers are in direct and obvious communication through a series of openings between the ends of the lamellae and situated in close relation to the peripheral wall of the pouches (Fig. 64). The width of the lamellae and chambers of the lateral walls is relatively considerably less in this species than in most of those described, and the width of the esophageal lumen in the frontal plane is correspondingly greater.

Helodrilus tetraedrus (Savigny) is widely distributed in various parts of the world and has several forms or varieties which have been recognized. An abundance of material has been available for study, both of the typical form which has spermiducal pores on somite 13, and of the form or variety *H. t. hercynius* which has the spermiducal pores on 15. Both forms are found in abundance in the banks of a small stream which flows through the campus of the University of Illinois. Other specimens of the typical form from the Puget Sound region, from Colorado, and from several of the North Central states have also been available for comparative study. In the preparation of a paper on the Lumbricidae of North America several years ago (Smith, 1917), the writer's attention was attracted by the very poorly developed condition of the gland in some specimens, while a much more

nearly normal condition was present in others. The thought that perhaps a more primitive condition of the organ might be represented in this species led to the preparation of sections of young specimens from cocoons, in the hope that they might throw light on the mode of origin of the gland. Instead of finding a series of folds appearing first and later a series of chambers formed by the fusion of the inner margins of the folds as was anticipated, the chambers were formed as tunnellike tubes from the beginning. It now seems more probable that something akin to a retrogression or degeneration of the organ is taking place in some specimens, at least. Some idea of the differences in the appearance of the organ in different individuals can be gained by a comparison of figures (45 and 46) from one specimen and figures (47 and 48) from another individual from the same locality.

The esophageal pouches in 10 are much larger in specimens which have the more extensive development of the longitudinal chambers (Fig. 47) and are smallest in specimens having the smallest chambers (Fig. 45). Something which may perhaps be reasonably construed as evidence of a sort of degeneration of structure, and which is found in each of the various specimens examined by the writer, is the presence of certain irregular cavities in close relation to the posterior part of the paired pouches in somite 10, and to the anterior ends of the longitudinal chambers in the esophageal wall near 10/11 (Fig. 55-57). Instead of there being a continuation of each of these chambers into the esophageal pouches in 10 and a direct communication there with the lumen of the esophagus, we find that most of the chambers and their separating lamellae terminate in these irregular cavities which in turn communicate with the pouch cavities through channels few in number when compared with the number of longitudinal chambers.

Peculiarities of the gland found in specimens showing different types of abnormalities will receive attention in another part of this paper (page 37).

Ribaucourt (1901) and Combault (1909) both gave attention to this species and referred to the lack of lateral enlargements of the gland posterior to the evaginated pouches in 10 ("diverticules de Perrier"). Combault's figure 22 which purports to be from a transverse section of the gland of this species represents the chambers as relatively much larger and fewer in number than they have been found in any of the writer's specimens. Ribaucourt's figure represents the chambers in a part of a section and indicates a number and shape of chambers much more nearly like those found in the American material.

Helodrilus chloroticus (Savigny) is a widely distributed species which has been found in large numbers in the banks of a stream in Urbana during the past few years, although it has not previously been reported in Illinois.

The pouches in somite 10 are more elongate, and their long axes more nearly approximate parallelism with the long axis of the esophagus than in most species (Fig. 49). Figure 50 is from a sagittal section and shows unusually well the continuity of each of the chambers through several somites, and of their cavities with that of the pouch to which they are related. Ribaucourt gives a brief description of the gland of this species and has a figure (1901, Fig. 60) which indicates rather elongate pouches, but is lacking in details.

Helodrilus caliginosus trapezoides (Dugès) is the most abundant and widely distributed of the earthworms found in the United States. The type form of the species together with the variety are collectively more abundantly represented in Europe than is any other species. They are found in most parts of the world where Europeans have settled.

The calciferous gland of the type form of the species has been described by Ribaucourt, Combault, and Stephenson and Prashad; and that of the form *trapezoides* by the first-named author. Combault gave a brief account and a figure of the gland of a form which he designated as *H. trapezoides*, but it is very different from any seen by the writer in specimens of that group.

A pair of large esophageal pouches are formed in 10, and on their posterior walls are found the anterior ends of the lamellae and chambers which are contained in the wall of the somites 11-14. A series of openings between the anterior ends of the lamellae in close relation to the peripheral walls of the pouches afford communication between the chambers and the pouch cavities as in several species described above. The number of wall chambers is usually 60 or more, and the lamellae separating the lateral chambers are relatively wide, with the result that the esophageal lumen is reduced to a rather narrow vertical cleft (Fig. 51). The vertical height of the lateral wall chambers is but a small fraction of the width in the plane of the lamellae and the cavities are narrow elongate clefts, widest towards the outer wall. In the outer and wider part of some of the chamber cavities, are longitudinal folds comparable to the outer parts of the lamellae in structure and in relations to the esophageal wall, but having their inner margins free. The width of these folds is highly variable but some of them increase in width posteriad and become lamellae with a resulting increase in the number of wall chambers. From about 60 or a few less near the anterior part of the gland, the number of chambers may increase posteriad to 65-70, there being individual variation in the numerical relations. The width of the lamellae separating the lateral chambers is somewhat reduced at the levels at which the septa join the gland wall, with an accompanying diminution in the diameter of the gland, but the variations in the dimensions of the different parts of the gland are not nearly as extensive as those in *Lumbricus terrestris* or in such forms as *Helodrilus lönnbergi*.

Octolasium lacteum (Örley) is a species which is widely distributed in both Europe and the United States and is reported from other parts of the

world where Europeans have settled. The calciferous gland was studied by Ribaucourt (1901) who interpreted it as equivalent to "la glande antero-posterieure IV" of the components of the gland as understood by him. He found nothing which he interpreted as equivalent to "les diverticules de Perrier." His figures indicate an organ very different from that found by the writer. A description of the latter follows. Combault has a figure of the gland which was probably based on one of the figures of Ribaucourt. It is on a larger scale and more diagrammatic.

The writer's first study of the gland of this species was based on Illinois specimens and the results were so different from those of the two writers above named that a study of European material seemed highly desirable. Fortunately specimens from Hamburg which had been identified and presented to the writer by Dr. Michaelsen were available and sections of two of them were made and studied with the result that marked similarity was found in the Illinois and European material. Perfectly definite esophageal pouches are formed in 10 in both the Illinois (Fig. 52) and European (Fig. 53) specimens. The wall chambers and separating lamellae are continued on the posterior and lateral walls of the pouches in a manner closely similar to that described in *Helodrilus gieseleri*, and the relations shown in certain sagittal sections from the part of the gland near its outer wall resemble closely corresponding sections of *H. chloroticus* (Fig. 50). Posterior to the esophageal pouches the gland extends through somites 11-14. The diameter is somewhat greater in 11 than in following somites, but there are no conspicuous enlargements like those of Lumbricus. The chambers of the lateral wall are wide enough to reduce the esophageal lumen to a narrow vertical cleft in the anterior somites. Of two specimens from which transverse sections were prepared, one had 46 chambers in 11 and the other one had 54. Serial sections from seven specimens of which two were from Europe were studied and very close agreement was found among them all.

It is somewhat difficult to account for the discrepancy between the above account and that of Ribaucourt who considered the gland in this species to be comparable to that of *H. oculatus* in the absence of esophageal pouches; and to be of a primitive type, though having thicker walls than had the gland of the last named species. The much enlarged lumen in the anterior part of the gland which is represented in his figure 62 and in that of Combault (1909, Fig. 21) suggests the possibility that the specimen studied may have happened to have had that part of the esophagus distended by a food mass which altered the general appearance. Deformations from such a cause are often encountered.

Sections from a specimen of *Octolasium transpadanum* (Rosa) from Europe have been available for study and an examination of sections through the gland shows that in this species there are perfectly definite esophageal pouches similar to those described above in *O. lacteum*.

There are several other North American species which have glands which are similar to those of such species as *Helodrilus gieseleri* and *H. beddardi*, and hardly merit separate descriptions and illustrations. Among such species are *H. tenuis*, *H. subrubicundus*, *H. zeteki*, and *H. longicinctus*. The glands of the two species last named contain about 60 wall chambers and the others about 40.

ESOPHAGEAL POUCHES AND OTHER LATERAL ENLARGEMENTS PRESENT

The species of a third group remain to be considered and are those which like the widely known *Lumbricus terrestris* have a type of gland which includes well differentiated esophageal pouches and in addition has conspicuous paired enlargements of the lateral chambered wall in each of somites 11 and 12. Several species of Lumbricus and also *Helodrilus octaedrus* are included in this group. This is the type of gland which has led to the frequent statements in text-books and elsewhere concerning the presence of three pairs of calciferous glands in the common earthworms.

Lumbricus terrestris Linnaeus. In view of the repeated references to the gland of this species in the earlier parts of this paper, a brief memorandum of the most important points will suffice. The esophageal pouches in 10 are large and definite with obvious openings into the lumen of the esophagus which are but little anterior to the septum 10/11. On their posterior and lateral walls are found the anterior ends of lamellae and wall chambers and the cavities of the latter communicate here with the pouch cavities. In each of the somites 11 and 12 the lateral portions of the chambered wall are much enlarged. Transverse sections from the middle of either of these somites show that the lateral lamellae and included chambers are much wider than in the neighboring somites or at the parts of the gland where the septa are attached. The relations are quite similar to those in the corresponding somites of *Helodrilus lönnbergi* (Fig. 25). In 13 and 14 the normal dimensions are regained and the gland is of more nearly uniform diameter. The number of chambers is commonly 60 or more with additional folds or partial lamellae attached to the wall in the outer margins of some of the chambers. In no case has the writer been able to find anything corresponding to the openings at the posterior end of these chambers which Harrington and Combault believed to be present and his observations corroborate those of Stephenson and Prashad.

Specimens of *Lumbricus rubellus* Hoffmeister and *Helodrilus octaedrus* (Savigny) from the United States and of *Lumbricus castaneus* (Savigny) from Denmark have been available for study and are found to agree in important characters of the calciferous glands with the description given above for the gland in *L. terrestris*. Ribaucourt reached similar conclusions from an examination of European material of *L. castaneus* and *H. octaedrus*.

CALCIFEROUS GLANDS IN ABNORMAL EARTHWORMS

An examination of a considerable number of abnormal specimens belonging to several species of Lumbricidae has resulted in finding that with certain types of irregularities in the other organs there are correlated certain abnormalities in the calciferous gland. Bilateral asymmetry in the positions of the various organs on the right and left sides of a specimen is a type of abnormality very frequently encountered. Two recent papers by Green (1923) and Smith (1922) contain accounts of three such specimens belonging to as many different species. In normal specimens of Lumbricidae in which esophageal pouches are formed, they are in the same somite (10) with the anterior spermaries (testes) and spermiducal funnels, and also with the "hearts" of the penultimate pair. Irregularities of metamerism that lead to inequalities in the numbers of somites on the two sides of a specimen, such for example as somite 10 on one side being opposite 9 or 11 of the other side, will usually be accompanied by asymmetry; the spermary, esophageal pouch, etc., belonging to 10 of one side will be opposite organs belonging to 9 or 11 of the opposite side. The appearance of such irregularities is perhaps due in part to the fact that each of the two lateral halves of the earthworm has its own developmental center. Although the two sides more commonly develop their quotas of any particular somite at the same time and of the same size, they do not necessarily or always so do.

Another type of irregularity is due to the tendency in occasional specimens to form supernumerary organs, as illustrated by the specimens described by Green (1923). She suggests in partial explanation that some disturbance in developmental processes has led to the development of two somites with contained organs from each of some of the units of developing tissue which would normally give rise to but a single somite. In specimens of this kind, more than one esophageal pouch may be formed on the same side of the specimen.

Figures 58 and 63 are from sections of two specimens with asymmetrical internal organs, but with normal metamerism, in so far as the septa and segmentation of the body wall are concerned. *Helodrilus tetraedrus* is frequently represented by specimens, some symmetrical and others asymmetrical, in which the contained organs are in somites other than the normal ones. Some of the varieties of this species which have been described without a study of the internal organization have presumably been based on such specimens.

An abnormal calciferous gland of an unusual type is found in an adult twinned specimen of *Helodrilus tetraedrus* which was described in a recent paper (Smith, 1924). The specimen is an example of twinning with a ventral type of union, and its general characters were summarized as follows: "The general organization is similar to what might be expected if one should succeed in splitting the anterior 45 somites of a normal individual in a sagittal plane from the mid-ventral surface as far as the middle of the lumen of the alimentary tract; then in spreading the cut surfaces apart and inserting a specimen similarly treated which had a corresponding length and number of somites (placing the cut surfaces in contact), thus producing a specimen with a double number of setae, reproductive organs, nerve and vascular trunks and nephridia, but with a single alimentary tract and mouth.

"The double or twinned condition prevails in the anterior 45 somites and is followed by about 70 somites of the type of organization found in the posterior part of a normal individual."

Paired evaginated pouches (Fig. 59 and 61) and related longitudinal chambers were present in the part of the esophagus derived from the larger individual, while the part which was derived from the smaller individual had paired invaginations in somite 10 (Fig. 60). One of the pouches of the larger individual was filled with calcareous concretions (Fig. 59) while the other one had none. The specimen was somewhat asymmetrical so that the two organs of a pair do not show in the same section. Figure 62 is from a section through the gland region in 11 and shows chambers of a type in which there is less reduction than in some normal specimens. It also shows sections of the two dorsal vessels, the two ventral vessels, and the two pairs of latero-longitudinal vessels which the twinned individual possessed.

MODE OF ORIGIN OF CALCIFEROUS GLANDS

Reference has already been made on page 16 to the peculiar views expressed by Harrington, and later advocated by Combault, in which the part of the gland posterior to 10 was assumed to have its origin in the greatly modified vascular layers of the esophageal wall; and that only the pouches in 10 are "lined with true epithelium and are developed as diverticula of the esophagus." Also on page 20 reference is made to the arguments of Stephenson and Prashad in support of the older view that the gland had its origin in a series of longitudinal folds involving the epithelium, and that these folds became higher and their inner edges fused, resulting in the formation of longitudinal tunnellike chambers. No such series of developmental stages is known among Lumbricidae of the present day. Such a series does exist however within a single genus of another family, the genus Diplocardia, and it was the discovery of species exhibiting the culmination of such a series that has led to the preparation of this paper.

The genus Diplocardia is peculiar to North America and has abundant representatives from the latitude of Northern Illinois to the Gulf Coast, and from the southeastern states westward nearly to the mountain states. At least one species is found in Mexico. About a dozen species are known and there are probably others.

Worms of the genus Diplocardia differ greatly from Lumbricidae, and among the differences the positions of certain organs may be mentioned. In Lumbricidae there is one gizzard in somites 17 and 18, in Diplocardia there are two gizzards, commonly in 5 and 6. In the former the clitellum is posterior to the spermiducal pores which are on 15, except in one form in which they are on 13; in Diplocardia the clitellum is anterior to the spermiducal pores which are commonly on 19 and rarely on 18 or posterior to 19. In Diplocardia the calciferous gland, when definitely formed, involves 14 and 15. In *D. communis*, the type species of the genus, and in other known species from the north central and western states, a few low longitudinal folds in 14 and 15 (Fig. 65 and 66) are all that represent a calciferous gland. In *D. michaelseni* from North Carolina (Smith, 1924a), definite folds in 14 and 15 are considerably higher (Fig. 67 and 68) than in the species from states farther north and west. In *D. eiseni* from Florida the folds in 14 and 15 are still higher (Fig. 69 and 70), some of them extending well towards the middle of the esophageal lumen, but the inner margins of the folds still remain unconnected with each other. In *D. floridana*, a new species from Florida described in another part of this paper, there are

numerous folds in 14 and 15 which have the inner margins of the highest folds connected by an epithelial layer (Fig. 78 and 79) in the anterior part of the organ. The folds have become separating lamellae forming the walls of short chambers which communicate freely with the lumen posteriorly, but not anteriorly.

In *D. mississippiensis*, a new species from Mississippi, also described in this paper, we find a still more highly developed series of folds which by fusion of inner margins become converted into separating lamellae and wall chambers (Fig. 71-73) which extend throughout the greater part of the organ. In the great number of the chambers and in their great width in the radial direction, we have an organ closely resembling the part of the gland found in 11 and 12 of some of the Lumbricidae with highly developed glands.

In view of the fact that various stages in the development of such a complex structure are represented in different species of the same genus, living contemporaneously, it seems to the writer that strong support is furnished for the view that the complex glands in Lumbricidae have had a similar mode of development.

DESCRIPTIONS OF TWO NEW SPECIES OF DIPLOCARDIA

DIPLOCARDIA MISSISSIPPIENSIS N. SP.

Four specimens collected in the spring of 1921 by H. R. Reed at McNeill, Mississippi, in soil on which carpet grass was growing, were received from C. V. Piper of the Bureau of Plant Industry at Washington, D. C. The specimens had been placed directly into the preservative without the use of anesthetics or fixing agents, and consequently are more or less contorted and strongly contracted. Each of three specimens was split in the median sagittal plane through approximately 25 anterior somites, and one half removed for sectioning. Transverse sections were made of the part belonging to the specimen which is designated as the type. Sagittal sections were made of the part from another specimen which will be known as paratype No. 1. Both halves of the anterior 24 somites were removed from the third specimen, designated as paratype No. 2, and transverse sections were made of one and sagittal sections of the other.

External Characters

These worms are relatively small in size. The type specimen has a length of 90 mm. and a maximum diameter of 2.5 mm. in the anterior part and is somewhat smaller posteriorly. The two paratypes are 81x2.5 mm. and 65x2 mm.; the diameter in each case being the maximum, and in the anterior part. The number of somites in the three specimens, given in the same sequence, is 148, 152, and 130. Nothing definite can be stated concerning the color, because of the method of preservation, but there is nothing that indicates much pigmentation or conspicuous coloration.

The setae are rather closely paired, but there is some variability in the spacing found in different somites of the same specimen and a little difference between the averages of different individuals. Using a, b, c, and d to represent setae on one side of a somite, beginning with a for the ventralmost one, we can represent the relative distances between the setae of the type specimen by the formula: aa:ab:bc:cd = 10:3:12:5. These figures are based on the averages of measurements of several somites. The two dorsalmost setae are nearly at opposite ends of a transverse diameter. In paratype No. 2, the setal distances are more nearly represented by the formula: aa:ab:bc:cd = 12:5:16:9. The setae a and b of somites 8, 9, and 10 are much modified in character in the three specimens studied. They are much longer and more slender than the ordinary setae, and the distal part is nearly straight and has the surface elaborately sculptured (Fig. 76).

In paratype No. 2, the setae of the ventral pairs on 11 are also modified in the same manner. The ventral setae of 18 and 20 are highly modified (penial setae) and closely associated with the distal part of the ducts of the prostate glands. They are extremely slender, somewhat curved and near the tip a little more strongly curved, while the tip itself seems slightly swollen. There is no evidence of surface sculpture. None of the specimens were at the height of sexual activity when preserved and the type specimen is the only one which has a well developed clitellum. It includes somites 13-18 and is nearly as thick on the ventral side as on the dorsal. Genital papillae are evident in the four specimens in the following situations: Surrounding each of the pairs of modified ventral setae in the spermathecal region is an area of thickened glandular epidermis. In each of these areas there is a rather extensive glandular development between the circular muscle layer and epithelium, quite similar to that described and figured by Eisen (1900, Fig. 154) in *Diplocardia udei* Eisen and stated by him to also occur in *D. michaelseni* Eisen. In three specimens, including the type, there are three pairs of such papillae on 8, 9, and 10. In paratype No. 2, a fourth pair is present on 11 associated with the modified setae of that somite, previously mentioned. A short transverse papilla is associated with the oviducal pores on 14, and another transverse papilla includes the two ventral bundles on 21. Prominent paired papillae are associated with the penial setae on somites 18 and 20, and the two papillae lying on either side of the median line are connected by a nearly straight longitudinal groove.

The position of the most anterior dorsal pore could not be determined with certainty since they are not always recognizable in the uncut specimens, and the part that was sectioned sometimes did not extend quite to the mid-dorsal line. Nothing was learned of the position in the type specimen. In paratype No. 2, a dorsal pore is recognizable at 11/12, and traces of what may be another one at 10/11 are present. None was found anterior to this position in any of the specimens. Nephridiopores are near the anterior border of the somites and dorsad of seta line d. The most anterior ones are in 2 and are dorsad of d by a distance greater than that between seta lines c and d, while the others are dorsad of d by a distance less than cd. The paired spermiducal pores are near the anterior border of 19, and in the longitudinal grooves which extend between the genital papillae on 18 and 20. The prostate gland pores are paired on 18 and 20 and are in close relation with the modified ventral setae of those somites. The oviducal pores are paired on 14. They are near the anterior border of the somite and mesad of seta line a. The spermathecal pores are paired on somites 8 and 9 in each of the four specimens examined, and paratype No. 2 has an additional one on one side of 7. Those of somite 8 are located ¼ to ⅓ of the length of the somite from the anterior margin and between setal lines a and b, but

usually nearer to the latter. The spermathecal pores of 9 in the type specimen are in about the same location with reference to the setae of that somite, as are those of 8 to the setae of 8, being at a considerable distance anterior to them. In each of the other three specimens examined, the pores on 9 are but slightly anterior to the ventral setae of that somite.

Internal Characters

Septa 8/9, 9/10, and 10/11 are the thickest and nearly equally developed; 7/8 and 11/12 are approximately two thirds as thick and the others much thinner. Two gizzards are well developed in somites 5 and 6, as in most known species of the genus. The walls of the esophagus in somites 9-13 have numerous short folds which fill up much of the lumen. They are richly supplied with branches from the blood plexus in the wall. The most interesting feature of the alimentary tract is the part in 14 and 15 which is more modified and complex in structure than in other known species of the genus. Sections show the structure of the walls to be comparable to that found in the part of the calciferous gland which is contained in somites 11 and 12 of most Lumbricidae. Figures 71 and 72 show some of the details of this structure. The widest of the numerous radiating longitudinal folds are united along their inner margins by an epithelial layer which includes a narrow secondary lumen. Posteriorly the numerous longitudinal chambers communicate with this lumen (Fig. 73). Cilia are especially numerous and well developed on the epithelial walls of the chambers near the outlets and presumably aid in propelling fluids from the chambers into the lumen. The gland is supplied with an extensively developed blood-vascular system which has several connections with the dorsal vessel. The alimentary tract in 16 is of relatively small diameter, and in 17 is abruptly widened and forms the anterior end of the intestine. The typhlosole begins in or near 18 and extends posteriad. Its general appearance in the first few somites is represented in figure 74 which is from a transverse section of somite 24. It includes a thin median layer continuous with the blood-vascular plexus in the body wall, and on each side of this a thickened epithelial layer continuous with that which bounds the intestinal lumen, but with the component cells fully twice as high as those of the intestinal wall. The vertical part which corresponds to the ordinary earthworm typhlosole extends at least to the middle of the lumen and is continued on each side of its distal margin into a fold lying approximately at right angles to the first, having a similar structure and appearance, and the two lateral folds having a combined width fully equal to that of the median part to which they are attached. This modified type of typhlosole is present in approximately fifteen somites of the anterior part of the intestine. Posterior to this part there is a reduction of the lateral wings and the appearance is more nearly like that of the ordinary earthworm typhlosole.

The circulatory system conforms closely to that already known in *Diplocardia eiseni* (Michaelsen). The dorsal vessel is single in the greater part of its course, except in a few somites in the clitellar region, where it is doubled between successive septa. A pair of large transverse vessels or "hearts" is present in each of somites 10 to 13. They are of the dorso-intestinal type, as are those of other Diplocardia species which the writer has had an opportunity to study. The chief connection of the dorsal ends of the hearts is with the richly developed vascular system of the esophageal wall and not with the dorsal vessel. There are frequent and extensive connections between the dorsal vessel and the vessels of the esophageal wall. In each of somites 7, 8, and 9, are much more slender "hearts" of ordinary type connecting the dorsal and ventral vessels. Such connecting vessels are often called dorsal hearts. In other Diplocardia species studied by the writer there is a definite continuous supra-intestinal blood vessel extending from somite 9 to 13 or 14, along the dorsal side of the esophagus, and between it and the dorsal vessel. With this vessel the dorso-intestinal hearts of such species have their chief dorsal connection. In the species here described such a continuous supra-intestinal vessel has not been identified and the chief dorsal connection of such hearts seems to be with the vascular plexus of the esophageal wall. It is possible that such a vessel may normally be present and the difficulty in finding it be due to the injuries occasioned in splitting the specimen preparatory to removing the sand from the alimentary tract in preparation for section cutting.

The nephridia are of the meganephric type and the first pair is in the second somite. The narrowed parts of the nephridial ducts which terminate in the nephridiopores exhibit in this species, with the exception of the first pair, a marked uniformity in their course; and in the level, with reference to the seta line d, at which they traverse the body wall. In tracing the duct from the nephridiopore, which is ordinarily slightly dorsad of seta line d, one finds that the course is directly through the outer epithelial layer; then slightly ventrad and posteriad in the circular muscle layer to the level of seta line d; and then through the longitudinal muscle layer to the coelomic cavity where it joins the main nephridial mass. The course through the longitudinal muscle layer is ordinarily between the two more or less definitely distinct bands of longitudinal muscle fibres which farther posteriad in the somite separate from each other, and extend one dorsad and the other ventrad of the corresponding d seta. These relations have been studied in only about 25 anterior somites.

The reproductive organs have characters commonly found in the genus. Spermaries and spermiducal funnels are paired in each of somites 10 and 11 and the sperm ducts of either side unite in 19 just before they open to the exterior. Paired sperm sacs in 9 and 12 open through septa 9/10 and 11/12 into somites 10 and 11 as in other species. The prostate glands of the an-

terior pair open to the exterior on 18, but occupy a great deal of space normally belonging to 18 and 19. Similarly those of the posterior pair open on 20, but extend into 21. In each of the three specimens sectioned, the duct of each prostate gland has a length nearly equal to half of the diameter of the worm and a circular muscle layer forms an important part of the wall. The duct extends dorsad and anteriad from its attachment to the body wall and enters the gland mass near the anterior septum. After its entrance into the gland, the lumen is traced with considerable difficulty, because of its very small diameter and the disappearance of the wall layers except a very inconspicuous epithelium. From its union with the duct, each gland extends dorsad and posteriad and then ventrad along the posterior septum, and then through the septum into the next following somite and again dorsad, filling a considerable part of the space between the intestine and body wall. The gland cells form many groups massed together and the secretion seemingly finds its way through very small inconspicuous passages to the main duct, itself very small, which extends through the middle of the gland from near its free end to the muscular walled duct which is its outlet. The structure of these glands seems to be very similar to that described by Eisen (1900) in *D. michaelseni* and *D. udei*. Ovaries and oviducal funnels are paired in 13 and the oviducts in 14. There are paired spermathecae in each of somites 8 and 9 in each of the specimens sectioned and in one of them, on one side of 7, is a spermathecal pore and a duct in the body wall which have a size and appearance similar to those of the corresponding parts of other spermathecae. A similar asymmetry in spermathecal development is noted by Michaelsen (1894, p. 189) in *D. eiseni*. Each spermatheca includes a rather long duct with a narrow lumen which opens into a large sac. Attached to the duct, somewhat nearer to the sac than to the spermathecal pore, is a cluster of a dozen or more small thin-walled chambers which communicate with each other and through several channels are also in communication with the lumen of the duct (Fig. 75). One such channel may afford communication for several chambers. In two specimens these chambers are filled with sperm cells.

DIPLOCARDIA FLORIDANA N. SP.

One specimen collected at Monticello, Florida, was received by the writer in January, 1914, while it was still living, and was preserved in good condition for study. It was not at a stage of sexual activity when collected and hence certain characters of the reproductive organs presumably differ somewhat from those of sexually active specimens. The anterior 22 somites were split in the median sagittal plane and longitudinal sections were made of the right half and transverse sections of the left half.

External Characters

The specimen is 98 mm. in length and varies in diameter from about 3 mm. in the anterior part to slightly more than 2 mm. posteriorly. The

number of somites is 159, but the last four somites have an appearance that suggests the possibility that regeneration may have been taking place.

The setae are all included in the ventral half of the worm, the dorsalmost ones being but slightly ventrad of the ends of the transverse diameter. There is considerable variation in the spacing of the setae in different somites, but the relative distances are approximately indicated by the following formula which is based on averages of measurements made on several different somites. aa:ab:bc:cd=8:3:8:5. The ventral setae of 8 and 9 are modified, but their characteristics have not been satisfactorily determined. Four are undeveloped and the other four were oblique to the plane of sectioning and only fragments are represented in any one section. Those examined are approximately 50% longer than setae of the ordinary type and scarcely more than two thirds as great in diameter. The distal end is nearly straight and is sculptured with extremely fine markings, very different in appearance from those of the corresponding setae of *D. mississippiensis* and *D. michaelseni*. There is of course no certainty that these setae are the same as those present at the time of sexual activity. The ventral setae of 18 and 20 are very small, slender, and much modified, but nothing can be determined concerning their sculpture.

There is almost no development of the clitellum nor of genital papillae. On the ventral side of 8 and 9, near the spermathecal pores, there are traces of gland development and a slightly thickened epidermal layer which indicate that paired genital papillae are present on those somites at the time of sexual activity. There are indications that they resemble the papillae similarly located in *D. mississippiensis*.

The first recognizable dorsal pore is at 10/11. The nephridiopores are at the anterior margins and the most anterior ones are in the second somite. 39 of the nephridiopores of the anterior 23 somites have been located and exhibit an unusual degree of variability in their position. Three are in seta line c; one between seta lines c and d; four in seta line d; the remaining 31 are dorsad of seta line d, but at varying distances. Using the symbol cd to indicate the average distance between the setae c and d, the locations of the nephridiopores dorsad of seta line d are about as follows: eleven of them are dorsad of line d by a distance less than cd, eleven of them at a distance about equal to cd, and nine vary from a distance about one and a half times cd to three times cd. The spermiducal pores are on 19, near the anterior margin, and nearly in seta line b. Each is borne on a very small papilla in a longitudinal groove extending between the prostate gland pores of the same side of the worm. The prostate gland pores are on 18 and 20 and open immediately posteriad of seta b of the same somites. The oviducal pores are paired on 14. They are anterior to the ventral seta bundles and mesad of seta line a. The spermathecal pores are paired on 8 and 9. Those of 8 are somewhat anterior to the ventral bundles and those of 9 are between the setae of the corresponding ventral bundles.

Internal Characters

Septa 8/9 and 9/10 are the thickest and about equally developed; septa 7/8, 10/11, and 11/12 are nearly as strongly thickened; 6/7 and 12/13 are much thinner, though slightly more developed than the remaining septa.

The alimentary tract is similar to that of other species of the genus in most respects. Two well developed gizzards are present in 5 and 6. In 9 to 13, inclusive, the inner layer of the esophagus has numerous short longitudinal folds which are richly supplied with blood. In 14 and 15 and chiefly in the latter somite, there is a more elaborate type of calciferous gland than any thus far described in the genus, except the one in *D. mississippiensis*, and it is scarcely less highly differentiated than the one in that species. Figures 78 and 80 will aid in the description of its anatomy. As in the last named species, there are numerous longitudinal folds of the inner layer of a much widened part of the esophagus, and the inner margins of the widest of these folds are connected by an epithelial layer that forms a secondary lumen (Fig. 78). This condition is found in the anterior part of the organ. As one follows the organ posteriad it will be noticed that the epithelial lining of the inner lumen becomes discontinuous on its lateral walls (Fig. 79), and that the spaces between the folds of these walls are continuous with that of the inner lumen. Still farther posteriad (Fig. 80) there is increasing discontinuity of the inner edges of the folds and a corresponding increase in the extent of the continuity of the spaces between the walls, and the disappearance of the definiteness of an inner lumen. No communications of the spaces between the folds with that of the secondary lumen are found in the part of the gland anterior to that represented by figure 78. The alimentary tract of 16 is relatively small in diameter with a few low folds. In 17 there is a marked increase in the diameter of the alimentary tract, forming what may be considered as the anterior end of the intestine. The wall of the anterior part of the intestine has an almost continuous layer of blood which has frequent connections with the dorsal vessel. The typhlosole (Fig. 81) is much like that of *D. mississippiensis*. In sections of somite 50 and of somite 100, the two lateral folds are still conspicuous, attached to the distal margin of the median fold which corresponds to the more common form of typhlosole found in ordinary earthworms. This triplicate type of typhlosole extends much farther posteriad than it does in *D. mississippiensis*.

The dorsal vessel is double between consecutive septa in somites 6–25 and single posterior to 25. A distinct supra-intestinal vessel is developed in 10–13. There are paired dorso-intestinal hearts in 10, 11, and 12 which unite the supra-intestinal and ventral vessels. Each of these hearts has a very small branch which joins the dorsal vessel. Dorsal

hearts which have their principal dorsal connection with the dorsal vessel and are smaller than the dorso-intestinal hearts are paired in 7–9.

The nephridia are of the ordinary meganephric type and the first pair, which are very small, are in the second somite. The narrowed part of the nephridial duct which terminates in the nephridiopore follows a fairly direct course through the body wall to the coelomic cavity and, since there is much variability in the locations of the nephridiopores with reference to the seta line d, there is a corresponding variability with reference to the seta line d in the levels at which the nephridial ducts traverse the longitudinal muscle layer of the body wall. But a small percentage of the ducts have their course between the two bands of longitudinal muscle fibers which are in contact in seta line d and which, in the immediate vicinity of the dorsal setae bundles, separate with one extending dorsad and the other ventrad of d.

Spermaries and spermiducal funnels are paired in each of the somites 10 and 11. The sperm ducts of either side extend posteriad between the circular muscle layer and the coelomic epithelium, and unite in somite 18. Paired sperm sacs are present in 9 and 12 and not in intervening somites. The prostate glands are present in 18 and 20. Those of 18 are confined to that somite and those of the posterior pair opening on 20 have a part of the glandular portion extending into 21. The glands are of reduced size but apparently have the same general type of structure as that described in *D. mississippiensis*. Ovaries and oviducal funnels are paired in 13 and oviducts in 14. Spermathecae are paired in 8 and 9 and are presumably smaller than at the season of sexual activity, and with accessory structures less highly developed. Apparently certain rudimentary bodies attached to the spermathecal ducts are the representatives of the thin-walled storage chambers described in *D. mississippiensis*.

D. floridana and *D. mississippiensis* are closely related to two other species from the southeastern part of the United States and with them form a group in which are found interesting structural deviations from the characters found in known species of other parts of the United States. *D. michaelseni* Eisen from North Carolina and *D. eiseni* (Michaelsen) from Florida are the two other forms under consideration. The interesting series of stages of increasing complexity in the folds of the inner layer of the esophageal wall of somites 14 and 15, culminating in the highly complex gland described in *D. mississippiensis*, which so closely resembles the calciferous gland of Lumbricidae has already been discussed. Other peculiarities of the group of species mentioned are the presence of specially modified ventral setae in the spermathecal somites and of a peculiar type of glands related to the outer ends of those setae. The location of the spermathecal pores in the somites bearing them tends to be farther posteriad in members of this group than in other species. The usual position of the pores in

other species is near the anterior margins of the somites, while in this group some or all of the spermathecal pores are near the ventral setal bundles, or still farther posteriad. The structure of the prostate glands in these species differs somewhat from that found in most others. This has been mentioned in the discussion of these organs in the preceding descriptions, and has been discussed at length by Eisen (1900, pp. 181 and 188) and also noticed by Michaelsen (1894, p. 188). In all four of the species the dorsal vessel is double between septa in most or all of somites 6–25 and single in the greater part of its course.

Eisen's description of *D. udei* indicates that that species is allied to the group in the possession of modified setae and associated glands in the spermathecal somites, and in the structure of the prostate glands, but not in the location of the spermathecal pores, in the character of the esophagus in 14 and 15, nor in having the dorsal vessel double in a part of its course.

The known distribution of the representatives of these closely related forms is limited to the relatively small territory which includes a few of the states in the southeastern part of the United States. This seems to give some support to the suggestion of Michaelsen (1894) that Diplocardia is a genus which phylogenetically is relatively young.

SUMMARY

The earliest important contribution to a knowledge of the anatomy of the calciferous glands in Lumbricidae was a paper by Leo in 1820. His ideas of the relations of the paired lateral enlargements of the esophageal wall to each other and to the lumen of the esophagus were more accurate than those of any subsequent writer prior to 1887, except those expressed by Henle, who in 1835 endorsed the views of Leo, but added nothing of significance. By the use of more refined methods in technique, Claparède in 1869 added much to the knowledge of the minute structure of the glands, but failed to gain as correct ideas of the general relations of the parts, as those of Leo. Most later writers, except Claparède, seem to have been unaware of the content of Leo's paper and have credited the later writers with the discoveries made by Leo.

Relatively few species of earthworms have glands of the type which is found in *Lumbricus terrestris* and which is the basis for the statements frequently made concerning the presence of "three pairs of glands." A greater number of species have a type of gland with but one pair of lateral enlargements, and these are in the tenth somite and correspond to the first "pair" in such species as *L. terrestris*. Several other species are found without any paired enlargements or pouches in the tenth somite, although a few of these may have one or two pairs in the next following somites.

Two new species of Diplocardia from the Gulf States are described, and in each of them, in somites 14 and 15, is found a type of gland which in structure and complexity strongly resembles the gland in Lumbricidae. A comparison of the gland structure in various species of Diplocardia discloses an interesting series of degrees in complexity beginning with the condition found in species from the latitude of Illinois, in which only a few low longitudinal folds are present in somites 14 and 15. More numerous and higher folds are found in a species from North Carolina, and a still further increase in number and height of folds is found in a Florida species. In the two new species the development of the gland has progressed still further, the inner edges of many of the folds becoming joined by a continuous epithelial layer with a resulting secondary lumen and a series of longitudinal tunnellike chambers, included between this lumen and the outer wall from which the folds developed. In view of the fact that various stages in the development of such a complex structure are represented in the different species of a single genus, living contemporaneously, there seems to be strong support for the contention that the complex glands in Lumbricidae have had a similar mode of development.

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PLATE I

EXPLANATION OF PLATE I

The figures on this plate are all from drawings made from figures in papers of some of the earlier writers on the calciferous glands of Lumbricidae. Only a part of the lettering has been reproduced.

Fig. 1 *Lumbricus terrestris*. Dissection showing sperm ducts and position of apertures. See footnote on page 12. From Leo (1820), Fig. VI.

Fig. 2 *Lumbricus terrestris*. Dissection of anterior part of alimentary tract showing openings into esophageal pouches. From Leo (1820), Fig. VIII.

Fig. 3 *Lumbricus terrestris*. Dissection showing calciferous gland and anterior part of alimentary tract. From Leo (1820), Fig. VII.

Fig. 4 *Lumbricus terrestris*. Part of esophagus with attached calciferous "glands." From part of figure by Morren (1829), Fig. 1, Plate XI.

Fig. 5 "Lumbrici minoris." As above, Morren (1829), Fig. 2, Plate XI.

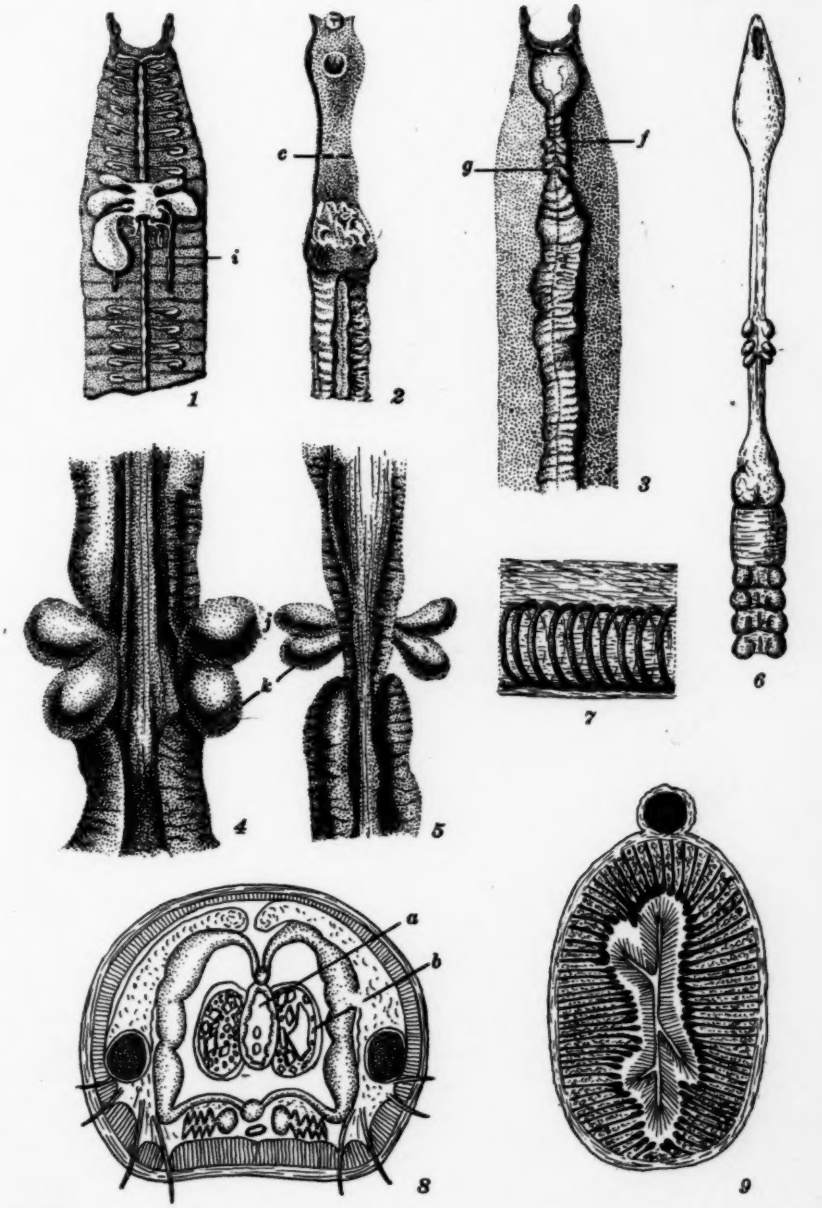
Fig. 6 Lumbricus. "Alimentary canal, removed from the other viscera." From Lankester (1864), Fig. 6, Plate VII. (*L. terrestris* and *L. agricola* were studied).

Fig. 7 Lumbricus. "Structure of oesophageal glands." From Lankester (1864), Fig. 2, Plate VII.

Fig. 8 *Lumbricus terrestris*. Transverse section passing through the esophageal pouches. From Claparède (1869), Fig. 1, Plate XLVIII.

Fig. 9 *Lumbricus terrestris*. Transverse section of gland, but not through enlargements in 11 and 12. From Claparède (1869), Fig. 1, Plate XLVI.

a lumen of esophagus
b esophageal pouch
c openings of esophageal pouches
f esophageal pouches
g gland enlargements
i sperm duct
j anterior gland enlargements
k posterior gland enlargements



SMITH GLANDS OF LUMBRICIDAE AND DIPLOCARDIA PLATE I

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PLATE II

EXPLANATION OF PLATE II

Fig. 10 *Helodrilus oculatus*. Transverse section of worm, passing through the anterior part of the gland in 10, and showing a few lateral wall chambers. ×36.

Fig. 11 *Helodrilus oculatus*. Transverse section of esophagus, slightly anterior to gland in 10.

Fig. 12 *Helodrilus oculatus*. Section of gland at 10/11. ×57.

Fig 13 *Helodrilus oculatus*. Section of gland near middle of somite 11.

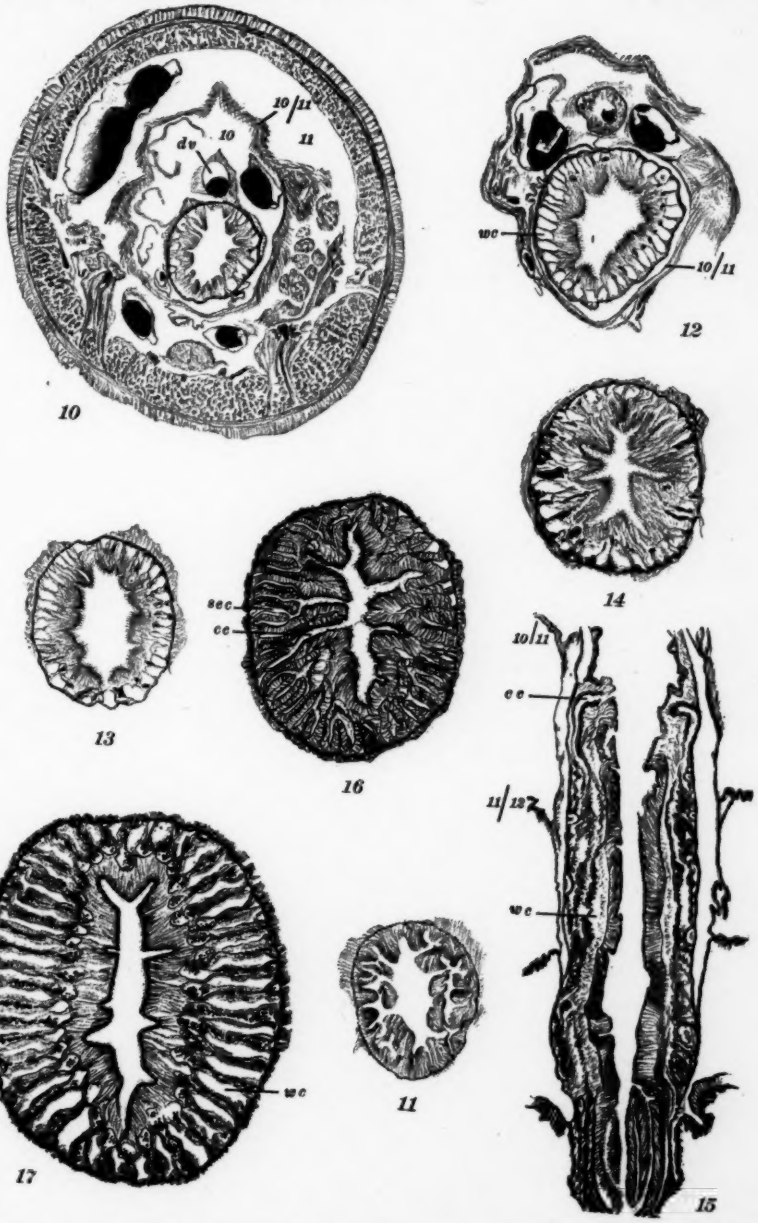
Fig. 14 *Helodrilus oculatus*. Section of gland at 13/14.

Fig. 15 *Helodrilus venetus hortensis*. Frontal section of gland in somites 11-13.

Fig. 16 *Helodrilus venetus hortensis*. Transverse section through the anterior part of the gland. ×112.

Fig. 17 *Helodrilus venetus hortensis*. Section through the gland at 11/12. ×112.

cc connecting channel
dv dorsal vessel
sec subepithelial cavity
wc wall chamber



SMITH GLANDS OF LUMBRICIDAE AND DIPLOCARDIA PLATE II

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PLATE III

EXPLANATION OF PLATE III

Fig. 18 *Helodrilus venetus*. Transverse section through the anterior end of the gland, and slightly oblique. ×36.

Fig. 19 *Helodrilus venetus*. Transverse section through the gland in somie 11. ×36.

Fig. 20 *Helodrilus foetidus*. Frontal section through the gland in somites 11-14. ×28.

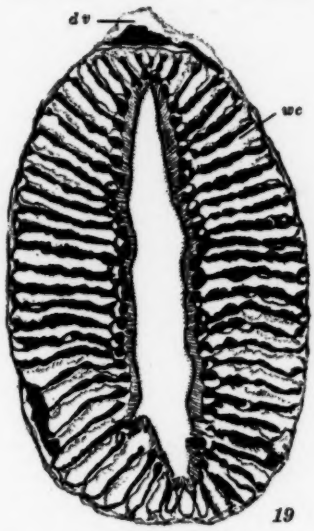
Fig. 21 *Helodrilus foetidus*. Transverse section through the anterior end of the gland in somite 11.

Fig. 22 *Helodrilus foetidus*. Section slightly posterior to that of figure 21. ×56.

Fig. 23 *Helodrilus foetidus*. Section of gland in posterior half of 11. ×56.

Fig. 24 *Helodrilus foetidus*. Section of gland in somite 12. ×36.

cc connecting channel
dv dorsal vessel
lv latero-longitudinal vessel
sec subepithelial cavity
vv ventral vessel
wc wall chamber



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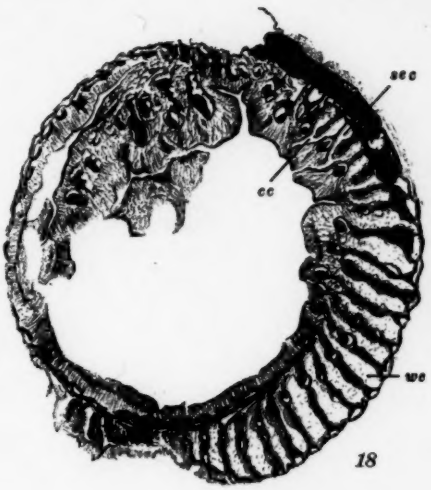

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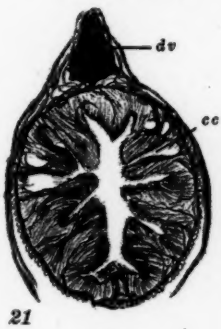

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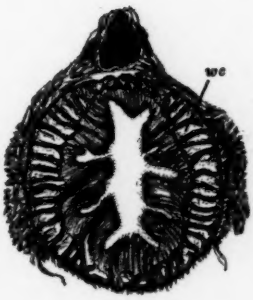

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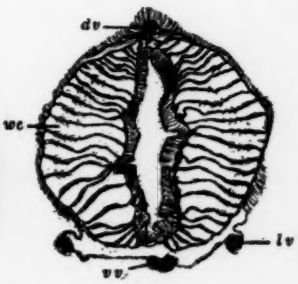

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SMITH GLANDS OF LUMBRICIDAE AND DIPLOCARDIA PLATE III

UNIV. OF MICH.

PLATE IV

EXPLANATION OF PLATE IV

Figures on this plate are all from sections of *Helodrilus lönnbergi*.

Fig. 25 Frontal section of anterior part of gland in somites 10-12. ×18.

Fig. 26 Frontal section of posterior part of gland in somites 13 and 14. ×18.

Fig. 27 Transverse section through anterior part of gland in somite 10. ×21

Fig. 28 Transverse section through the worm and passing through the gland in somite 11. ×11.

Fig. 29 Part of a section through the wall of the gland near the anterior part of somite 11 showing calcareous granules and gland structure. ×56

Figure 82 belongs with this series.

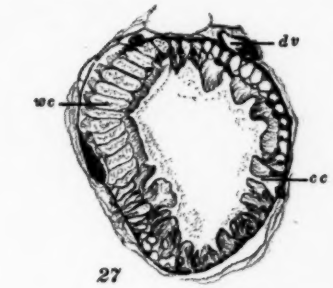
cc connecting channel

cg calcareous granules

dv dorsal vessel

l lamella

wc wall chamber



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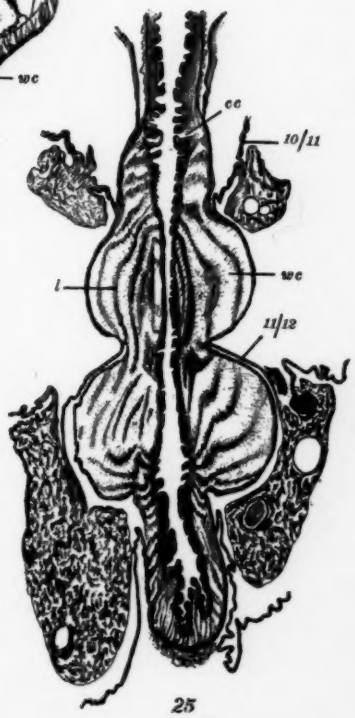

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SMITH GLANDS OF LUMBRICIDAE AND DIPLOCARDIA PLATE IV

UNIV OF MICH.

PLATE V

EXPLANATION OF PLATE V

Fig. 30 *Helodrilus palustris*. Frontal section of anterior part of gland in somites 10-13. ×36.

Fig. 31 *Helodrilus palustris*. Sagittal section through chambers in gland wall in somites 10 and 11. ×56.

Fig. 32 *Helodrilus palustris*. Small part of section (Fig. 31) more highly magnified to show channel connecting the cavity of a wall chamber with that of the esophageal pouch. ×250.

Fig. 33 *Helodrilus gieseleri*. Frontal section of gland in somites 10-15.

Fig. 34 *Helodrilus gieseleri*. Transverse section through esophageal pouches near anterior ends of lamellae. ×36.

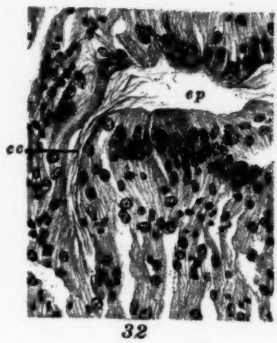
Fig. 35 *Helodrilus gieseleri*. Section slightly posterior to that of figure 34, showing a few chambers.

Fig. 36 *Helodrilus gieseleri*. Section still farther posterior, showing more chambers.

Fig. 37 *Helodrilus gieseleri*. Sagittal section through an esophageal pouch showing communication of pouch and chamber cavities. ×56.

Fig. 38 *Helodrilus gieseleri hempeli*. Section showing the same relations as in figure 37. ×90

cc connecting channel
ep esophageal pouch
l lamella
wc wall chamber



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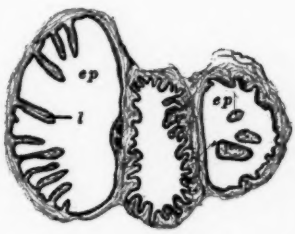

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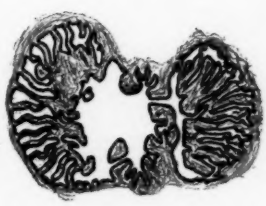
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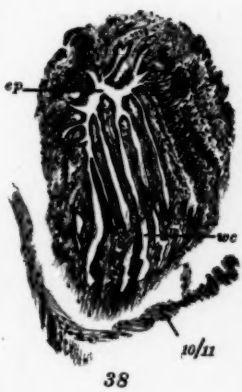

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SMITH GLANDS OF LUMBRICIDAE AND DIPLOCARDIA PLATE V

UNIV OF MICH.

PLATE VI

EXPLANATION OF PLATE VI

Fig. 39 *Helodrilus beddardi.* Frontal section of gland in somites 10 to 14.

Fig. 40 *Helodrilus beddardi.* Transverse section through the esophageal pouches showing unusually wide lamellae and chambers. ×56.

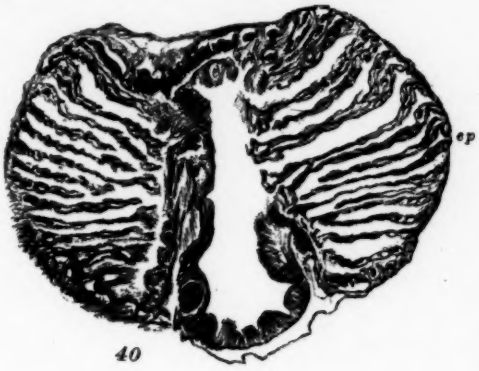
Fig. 41 *Helodrilus roseus.* Frontal section of gland in somites 10 to 14.

Fig. 42 *Helodrilus roseus.* Sagittal section through esophageal pouch near outer wall. ×48.

Fig. 43 *Helodrilus roseus.* Sagittal section from same specimen as above, but farther mesad. ×48.

Fig. 44 *Helodrilus parvus.* Frontal section of gland in somites 10 to 14.

ep esophageal pouch
l lamellar fold
wc wall chamber



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SMITH GLANDS OF LUMBRICIDAE AND DIPLOCARDIA PLATE VI

PLATE VII

EXPLANATION OF PLATE VII

Fig. 45 *Helodrilus tetraedrus*. Frontal section of gland in a specimen in which the chambers are much reduced in width. ×28.

Fig. 46 *Helodrilus tetraedrus*. Transverse section of gland in a specimen similar to one in figure 45. Epithelium poorly preserved. ×56.

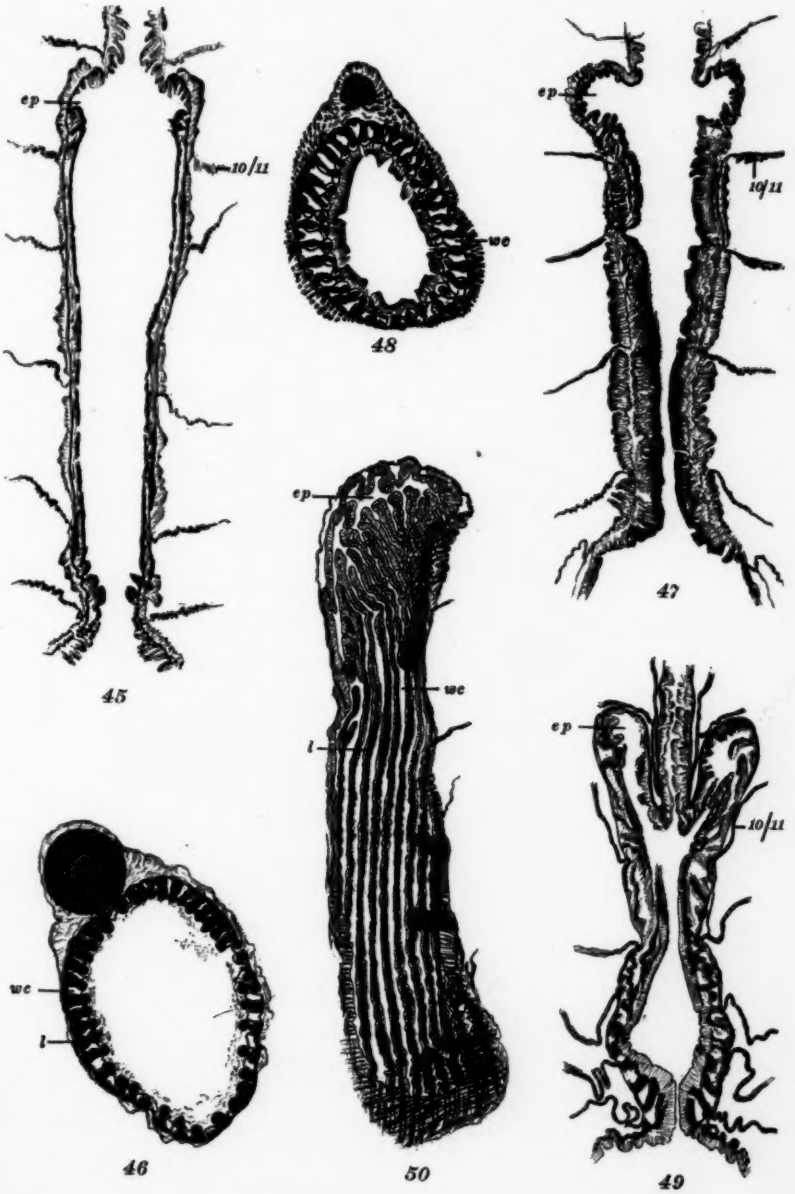
Fig. 47 *Helodrilus tetraedrus*. Frontal section of gland in a specimen in which the chambers are better developed than in the one in figure 45. ×28.

Fig. 48 *Helodrilus tetraedrus*. Transverse section of gland in a specimen similar to one in figure 47. ×56.

Fig. 49 *Helodrilus chloroticus*. Frontal section of gland in somites 10-14.

Fig. 50 *Helodrilus chloroticus*. Sagittal section of gland in 10-13, passing through chambers near outer wall and showing continuity of cavities of chambers and pouch. ×36.

ep esophageal pouch
l lamella
wc wall chamber



SMITH GLANDS OF LUMBRICIDAE AND DIPLOCARDIA PLATE VII

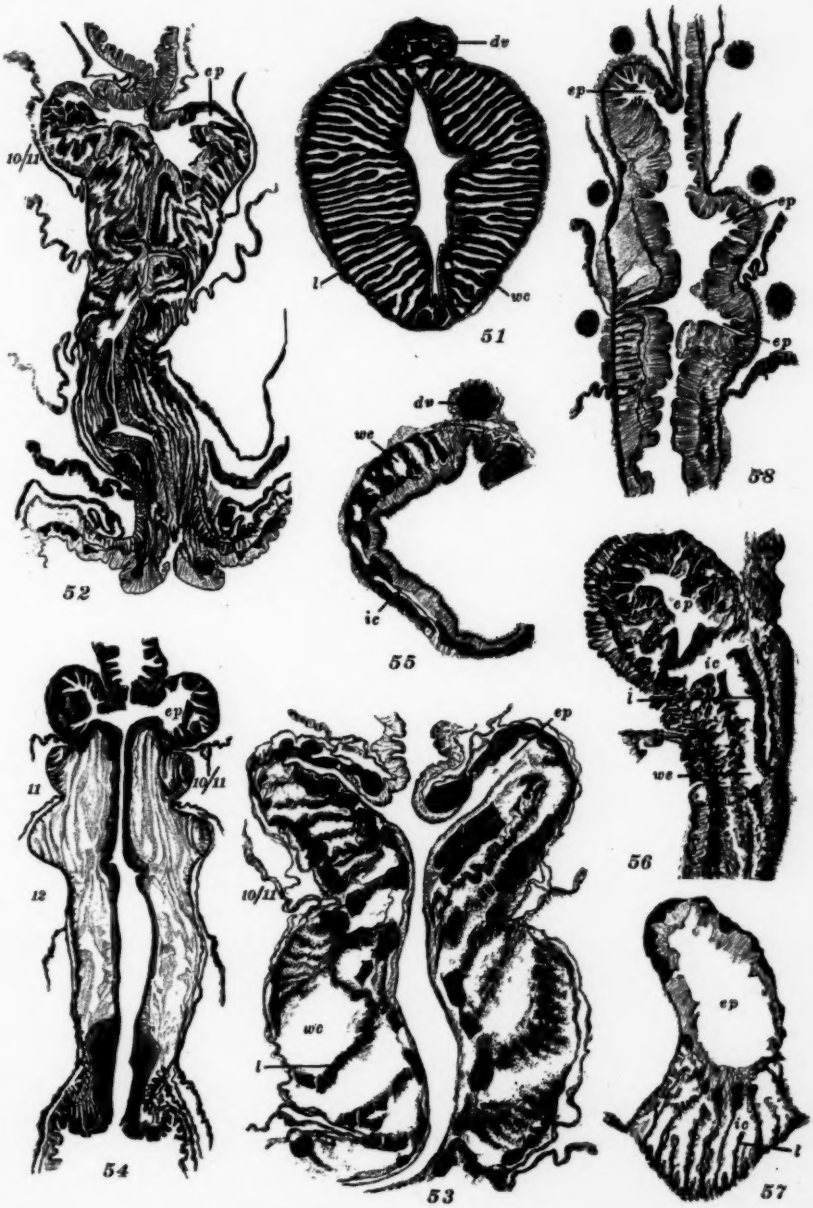
UNIV. OF ILL. OHIO

PLATE VIII

EXPLANATION OF PLATE VIII

Fig. 51 *Helodrilus caliginosus trapezoides*. Transverse section of gland in somite 11. ×28.
Fig. 52 *Octolasium lacteum*. Frontal section of gland in somites 10-14. ×18.
Fig. 53 *Octolasium lacteum*. Frontal section of anterior part of gland in somites 10 and 11 in a European specimen which was strongly contracted. ×36.
Fig. 54 *Lumbricus terrestris*. Frontal section of gland in somites 10-15. ×11.
Fig. 55 *Helodrilus tetraedrus*. Transverse section of gland slightly posterior to esophageal pouch and through irregular cavity in wall. ×64.
Fig. 56 *Helodrilus tetraedrus*. Frontal section of gland, showing chambers entering irregular cavity in wall near the esophageal pouch. ×64.
Fig. 57 *Helodrilus tetraedrus*. Sagittal section of gland, showing similar structure to that mentioned in figure 56. ×64.
Fig. 58 *Helodrilus caliginosus trapezoides*. Frontal section of gland in abnormal specimen.

dv dorsal vessel
ep esophageal pouch
ic irregular cavity
l lamella
wc wall chamber



SMITH GLANDS OF LUMBRICIDAE AND DIPLOCARDIA PLATE VIII

UNIV OF MICH.

PLATE IX

EXPLANATION OF PLATE IX

Fig. 59 *Helodrilus tetraedrus*. Transverse section of twinned specimen, through esophageal pouch of one side of larger individual. ×28.

Fig. 60 *Helodrilus tetraedrus*. Section of gland of above specimen, through invaginated pouch of smaller individual and anterior part of chambered wall on one side of larger individual.

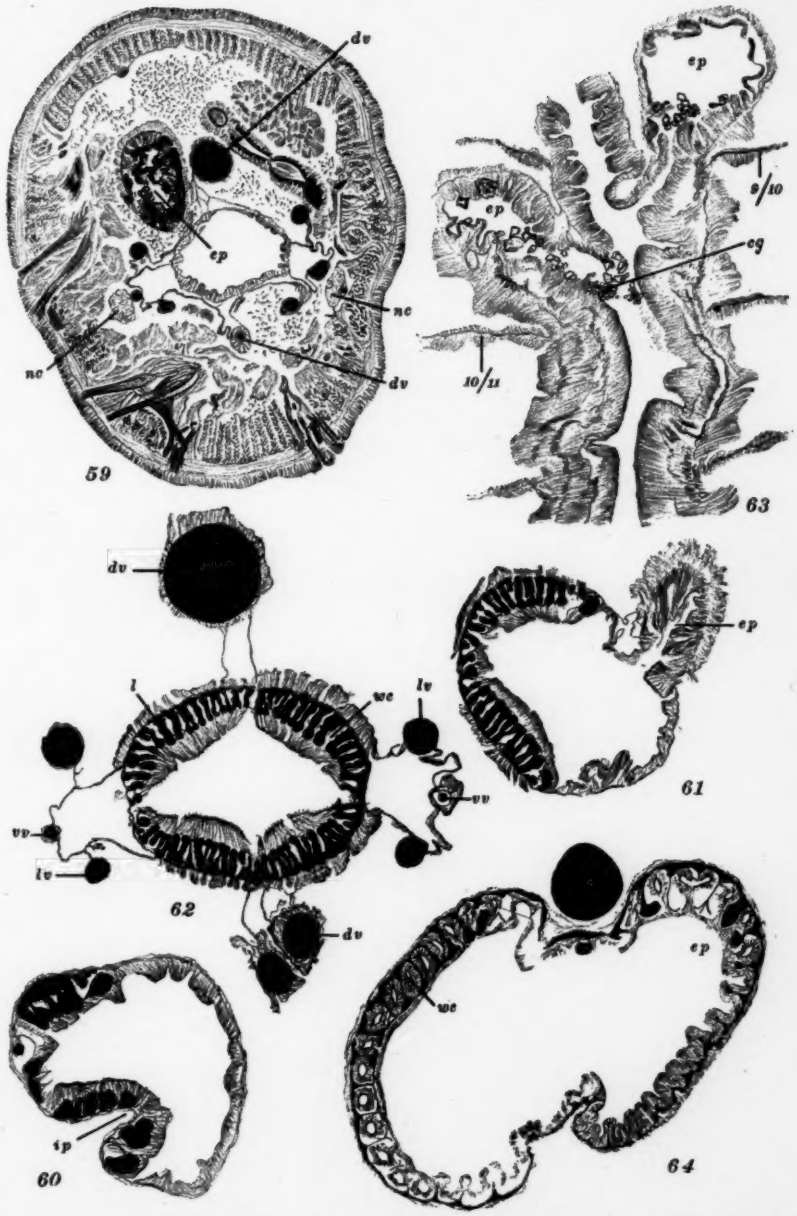
Fig. 61 *Helodrilus tetraedrus*. Section of gland of above specimen, through other esophageal pouch of larger individual and through wall chambers of opposite side in both individuals. ×56.

Fig. 62 *Helodrilus tetraedrus*. Section of gland of above specimen, showing wall chambers and lamellae of both individuals. ×56.

Fig. 63 *Helodrilus tetraedrus*. Frontal section through anterior part of gland in abnormal specimen with asymmetrical organs.

Fig. 64 *Helodrilus roseus*. Transverse section through the esophageal pouches near the anterior ends of the wall chambers. Transition from lamellae to folds and communication of chamber and pouch cavities are illustrated. ×68.

cg calcareous granules
dv dorsal vessel
ep esophageal pouch
ip invaginated pouch
l lamella
lv lateral vessel
nc nerve cord
vv ventral vessel
wc wall chamber



SMITH GLANDS OF LUMBRICIDAE AND DIPLOCARDIA PLATE IX

UNIV OF MICH.

PLATE X

EXPLANATION OF PLATE X

Fig. 65 *Diplocardia communis*. Transverse section through folds of esophagus in somite 14. ×36.

Fig. 66 *Diplocardia riparia*. Transverse section through folds of esophagus in somite 14. ×36.

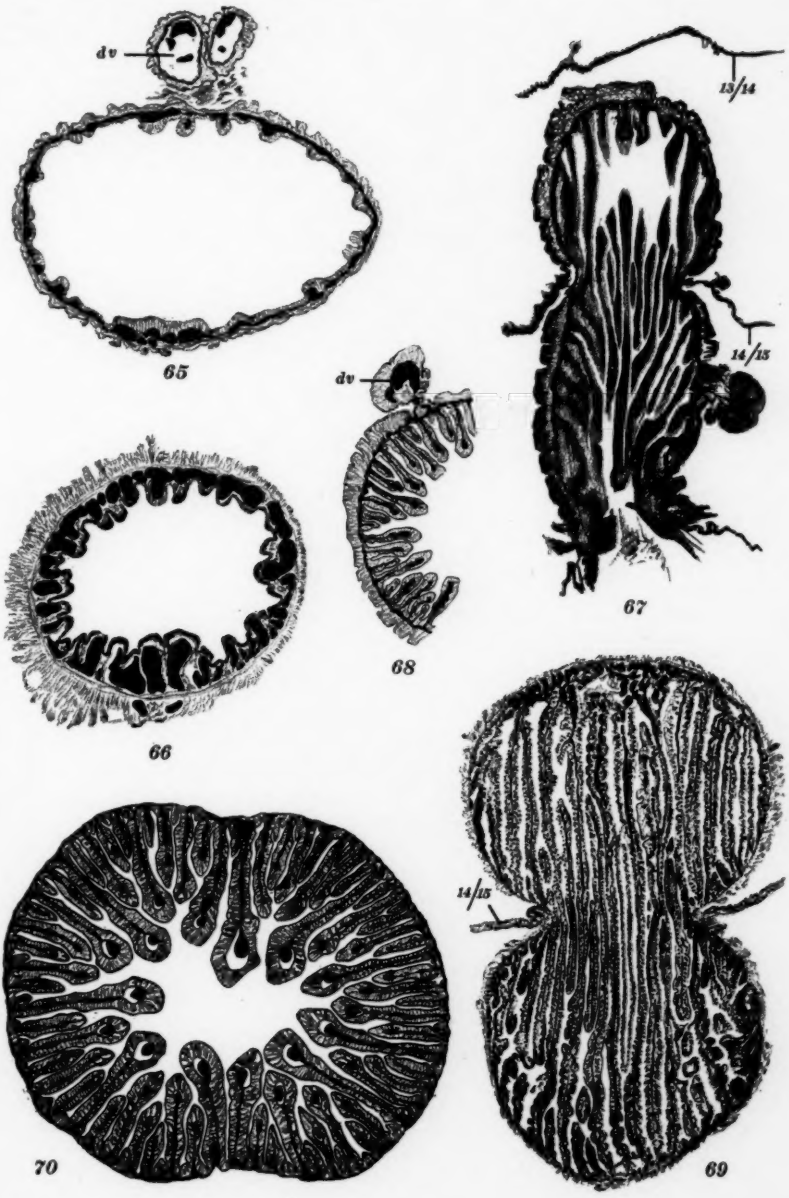
Fig. 67 *Diplocardia michaelseni*. Frontal section through gland in somites 14 and 15.

Fig. 68 *Diplocardia michaelseni*. Transverse section through gland in somite 14.

Fig. 69 *Diplocardia eiseni*. Frontal section through gland in somites 14 and 15.

Fig. 70 *Diplocardia eiseni*. Transverse section through gland in somite 14.

dv dorsal vessel



SMITH GLANDS OF LUMBRICIDAE AND DIPLOCARDIA PLATE X

UNIV. OF WIOH.

PLATE XI

EXPLANATION OF PLATE XI

Figures on this plate are all from *Diplocardia mississippiensis* n. sp.

Fig. 71 Frontal section through calciferous gland in somites 14 and 15.

Fig. 72 From a transverse section through median part of gland showing parts of gland and body wall and their relative size. ×35.

Fig. 73 From a transverse section through the gland near its posterior end. Only one side of gland is shown. ×48.

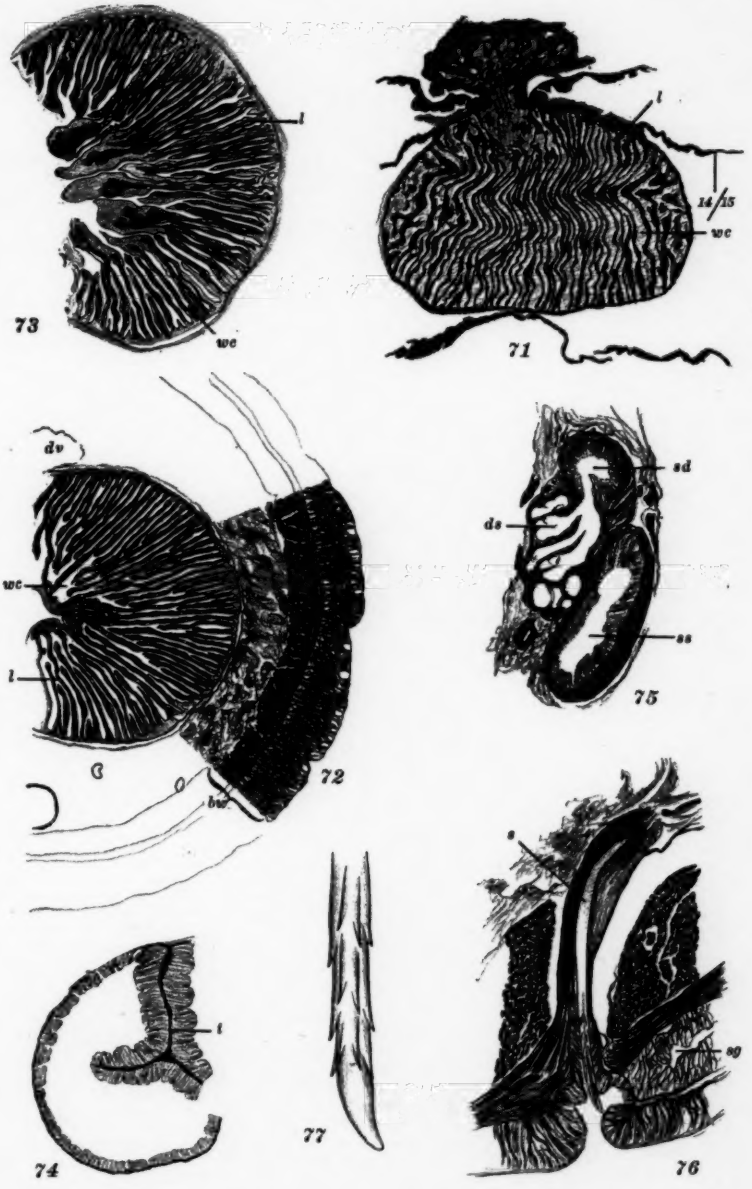
Fig. 74 Transverse section through the intestine in somite 24 showing the typhlosole. A part of the intestine had been removed. ×36.

Fig. 75 From a section through a spermatheca showing the accessory sacs attached to the duct. ×56.

Fig. 76 Transverse section, showing modified seta b of somite 8 and related structures. ×105.

Fig. 77 Distal end of modified seta b of somite 10.

bw body wall
ds sacs of spermathecal duct
dv dorsal vessel
l lamella
s modified seta
sd spermathecal duct
sg setal gland
ss spermathecal sac
t typhlosole
wc wall chamber



SMITH GLANDS OF LUMBRICIDAE AND DIPLOCARDIA PLATE XI

UNIV. OF MICH.

PLATE XII

EXPLANATION OF PLATE XII

Fig. 78 *Diplocardia floridana* n. sp. Transverse section of part of wall of anterior part of calciferous gland in somite 14. ×56.

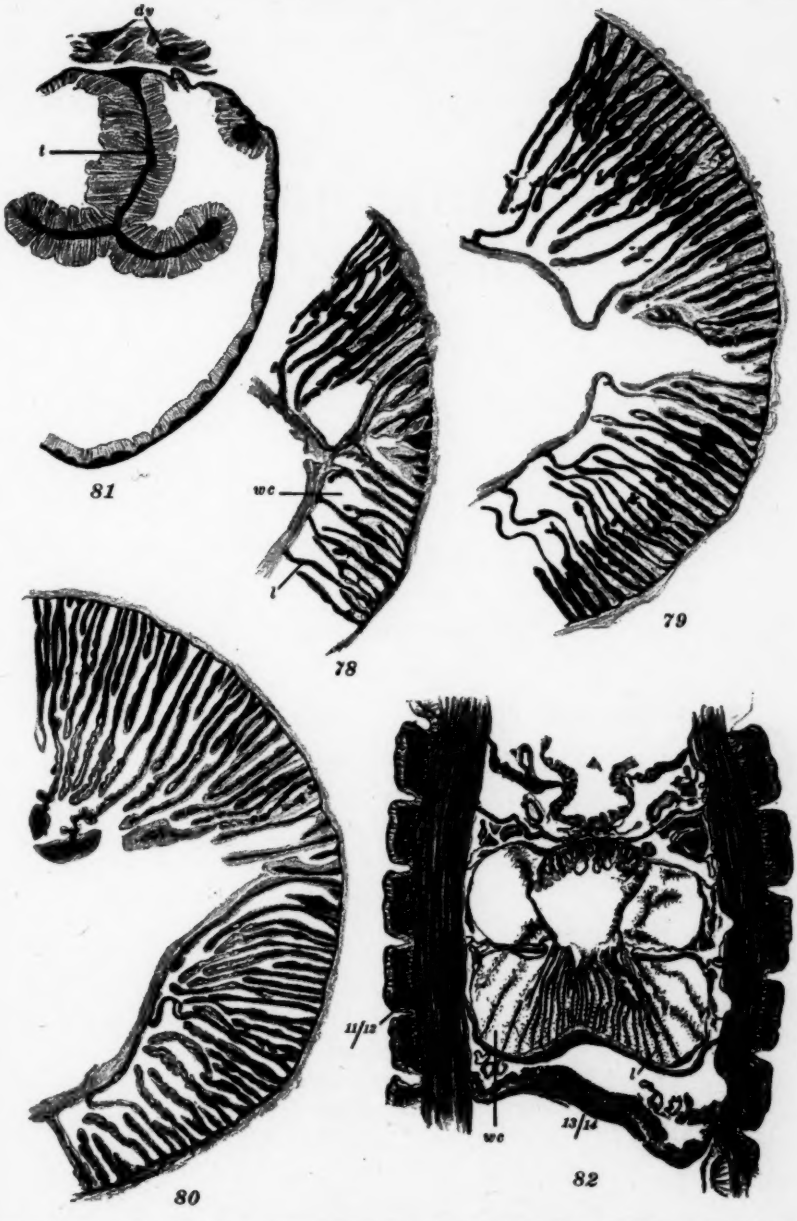
Fig. 79 *Diplocardia floridana*. Transverse section a little posteriad of the one in figure 78.

Fig. 80 *Diplocardia floridana*. Transverse section of gland near posterior end in somite 15.

Fig. 81 *Diplocardia floridana*. Transverse section of part of intestine in somite 22. ×36.

Fig. 82 *Helodrilus lönnbergi*. Frontal section through part of gland in an immature specimen, showing large size of gland in somites 11 and 12. This figure belongs with the series numbered 25-29. ×20.

dv dorsal vessel
l lamella
t typhlosole
wc wall chamber



SMITH GLANDS OF LUMBRICIDAE AND DIPLOCARDIA PLATE XII